

***Juglans* spp., juglone and allelopathy**

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1. INTRODUCTION

The "walnuts" are referable to *Juglans*, a genus of 20-25 species with a natural distribution across the Northern Hemisphere and extending into South America. *Juglans* is a member of the family Juglandaceae which contains 6 or 7 additional genera including *Carya*, *Cryptocarya* and a total of about 60 species. Walnuts are commercially important as the source of the edible walnut, the highly prized timber and as a specimen trees. Eating walnuts are usually obtained from *J. regia* (the common or Persian walnut, erroneously known as the English walnut) - a native of SE Europe and Asia, which has long been cultivated, but are also sometimes available locally from other species such as *J. nigra* (back walnut) - a native of eastern North America and *J. major*, *J. californica* and *J. hindsii*, native to the western U.S.

Grafting of superior fruit-bearing scions of *J. regia* onto rootstocks of hardier species, such as *J. hindsii* or *J. nigra* is common practice. The species of walnuts are in need of revision, particularly those from South and Central America, and from East Asia, as more than 60 species have been recognised in the past. At present about 20-25 species and numerous varieties are recognised; the better known species are listed in Table 1.

Table 1. Major species of *Juglans* (compiled from various sources)

Species	Common name	Distribution
Europe/Asia		
<i>J. regia</i> L.	Common or Persian walnut	S.E. Europe, Asia; widely planted
<i>J. mandshurica</i> Maxim.	Manchurian walnut	N.E. Asia
<i>J. ailanthifolia</i> Carrière	Japanese walnut	Japan, Russia
<i>J. cathayensis</i> Dode		China
North America/South America		
<i>J. nigra</i> L.	Black walnut	E.US; widely planted
<i>J. cinerea</i> L.	Butternut or white walnut	E.US and Canada
<i>J. major</i> (Torr.) Heller	Arizona walnut	S.W.US, Mexico
<i>J. microcarpa</i> Berl.	Little walnut or Texas black walnut	S.W.US
<i>J. hindsii</i> (Jepson) Jepson	Claro or N.California walnut	California
<i>J. californica</i> S. Wats.	California walnut	California
<i>J. olanchana</i> Standl. & Williams	Central American walnut	Mexico, Central America
<i>J. mollis</i> Engelm. ex Hemsl.		Mexico, Guatemala
<i>J. pyriformis</i> Liebman		Mexico
<i>J. jamaicensis</i> C. DC	Nogal or West Indies walnut	West Indies
<i>J. australis</i> Griseb.	Argentina, Bolivia	
<i>J. neotropica</i> Diels	Ecuador, Colombia	
Hybrids		

J. intermedia = *J. nigra* × *J. regia*

J. quadrangulata = *J. cinerea* × *J. regia*

Since antiquity, the walnut tree is known as a source of substances harmful to other living things. For example, rotting fruits were used by native North Americans to stun fish and decoctions of leaves have long been used by fishermen to drive worms to the soil surface. Many American folk uses for walnut, including foliage as a repellent for ants and flies, have been described (313). Such was the baneful reputation of the walnut in parts of Italy, that it is called "witches' tree" (302). However, walnut also provides amongst the earliest recorded suggestions of allelopathy and to this day walnut provides the best paradigm of allelopathy, which has attracted much attention from the popular press (34, 63, 95, 215, 251) and community service programs (99, 126, 138, 139).

2. HISTORICAL BACKGROUND

Early writings about the walnut concern the Old World species *Juglans regia*, the common or Persian walnut. The earliest recorded statement regarding the harmful effects of the walnut trees came from the Roman author Varro (309), writing in about 36 B.C.: "*If, for instance, he [your neighbour] has an oak-grove on the common boundary, you would be wrong to plant olive trees on the edge of such a wood, for these trees have a natural antipathy to it so great that, not only do they bear worse, but even, in their efforts to escape, bend away inwards toward the farm precisely as does the vine if planted near cabbage. Like oak trees, walnut trees near your farm, if of large size and standing at little distance from one another, make its margins totally unproductive.*" Pliny (224) further expanded on this: "[The shade] of the walnut is heavy and even causes headache in man¹ and injury to anything planted in its vicinity." and "*To each kind of plant shade is either a nurse or else a step-mother - at all events for the shadow of a walnut tree or a stone pine or a spruce or a silver fir to touch any plant whatever is undoubtedly poison.*" He also notes that: "*The oak and the olive are parted by such inveterate hatred that if one be planted in the hole from which the other has been dug out, they die, the oak indeed also dying if planted near the walnut.*"

These notions were commonly reiterated and sometimes augmented in subsequent natural history and agricultural tracts in the Medieval period. Of particular interest is the Andalusian region which had a rich history of agricultural writers beginning with Columella. The Arab world had a number of great libraries as the Arabs, unlike the Europeans, had access to paper; however, the vast majority of the books were burnt during the Christian purges of the 15th and 16th centuries. Arabic science, mainly under the influence of Jabir ibn Hayyam, developed a complex system of antipathies and sympathies, based largely on supposed compositions of things from

the elements of water, air, earth and fire (161). The few surviving agricultural writings from this era seem to have a more practical basis. The writings of the 12th century Andalusian writer Ibn Al-Awwam were largely based on a number of predecessors but these works, notably that of the 10th century Persian, Ibn Wahshiyya have printed been recently. *al-Filaha al Nabatiyya* or Nabathean Agriculture, compiled by Ibn Wahshiyya, may owe its origins to ancient Babylonian writings and, thus, predate Greek and Roman writings, but the earliest known version in Arabic dates to the 8th century. Ibn Wahshiyya (137) states numerous plant sympathies and antipathies but these commonly retain an occult influence. In describing the walnut he says that it is "*the opposite of the pomegranate with respect to cold and heat. It is mostly hot.*" In the context of the era, the references to "heat" likely relate to the bitterness (juglone), as later it is stated: "*it is rare for the walnut to be attacked by diseases because the tree is strong, hard and hot and thus can protect itself from disease and weakness.*" and "*It is harmful because the heat of its fruit is intense and the heat causes pimples and black marks.*" Ibn Al-Awwam's work, while important in his era, was effectively lost until the 19th century when translations appeared in Spanish (135) and French (136), although it was evidently known to the 16th century writer, Herrera (129). Ibn Al-Awwam wrote of the walnut (translated from 136): "*All trees planted in the vicinity demonstrate antipathy, with the exception of the fig, which is found to have several points of agreeability.*"

Hadj of Grenada says "*That the walnut is antipathetic to most trees that one wishes to plant in its vicinity, except the fig and the mulberry, because the walnut is of excessive scorching and dryness, which is harmful to all which come near it and which are not sympathetic to it. It destroys everything which grows beneath it, except certain winter plants, or ferny plants, which one can grow beneath its branches when it is bare of its leaves; when one wants to associate with climbing grapevines, they do not succeed at all and fail at the utter limit of enfeeblement.*"

The 13th century writer Albertus Magnus (2) described the walnut as unfavourable to surrounding cultivated plants because of its "*indwelling extreme toxic bitterness*". Pietro di Crescenzi in his work *Agricoltura Commodorum* (62), written in 1304 and printed in 1471, stated that walnuts were harmful to surrounding trees. Cardano (48) attributed the harmful effects of walnut to the shade-assisted accumulation of "*vapours*".

The writings of Pliny and other Latin authors were compiled and augmented with information from Ibn Al-Awwam and other Hispano-Arabic writers by Herrera (129). He records that the Castilian name for walnut has the meaning of "to harm", although it is now generally regarded that Romance language names for walnut such as *nogal* (Spanish), *noyer* (French) and *noce* (Italian) are derived from the Latin *nux* for nut. This etymological misconception is paralleled in English, with the term

“noxious” derived from the Latin *noxa*, meaning harm. Curiously, Fuchs (94) in 1550 claimed that the unrelated Greek word for walnut *karyon* was also derived from a word meaning causing headache.

The first indication of controversy concerning the harmful effects of walnut appears in 1664 in the writings of Evelyn (86). Evelyn was a great proponent of planting walnut in England and he described how, in Burgundy, where walnut is planted in wheat fields by farmers, “*It is so far from hurting the crop, that they look on them as a great preserver, by keeping the ground warm.*” However, farmers in Burgundy avoid planting grapes beneath walnut (183).

A significant advance on walnut toxicity appears in the writings of Worlidge (330) in 1677, as he provides a statement of the mechanism of injury, some two hundred years prior to the often quoted statements of Stickney and Hoy (281). Worlidge writes: “*There is a sympathy and antipathy in plants. And many fabulous traditions there are concerning them, but this is certainly observed that some trees will not thrive under the shade or drip of another, as the drip of a walnut tree and of a cherry are injurious to other trees, because the leaf is bitter and the drip destroyeth such trees or plants that are under it.*”

Well indicative of knowledge of the walnut in Europe in the seventeenth century, and the way in which Pliny’s information was augmented, is the account of Estienne (85), who regards the French term for walnut as also meaning “harmful”: “*The walnut is a species common enough in all parts, & known to bear such a name [noyer] because it is noxious to others which are neighbouring, in the places where it is planted, & and to people & even to babies, all the more one sees by experience, that if a man sleeps below, he will wake up with great heaviness of the head and so stunned that he nearly cannot move himself. And its shade is so bad that nothing good can grow underneath there, & that also the roots are of marvellous extent, which spoils all the land where this tree is situated & planted. Thus it should not be planted in a workable field, and especially in those which are richest and most fertile, rather towards the North, on the side of roads or elsewhere, where there are no other fruits which can receive damage from this tree. To place a tree of another species among them, it is not any more useful than putting a little artisan among two great lords: for walnut trees which are naturally great miners with their large roots, remove its food even in a trench, & the cover from its above blocks the sun, & the liberty of the air also: but because the things of this world are thus composed, there is not anything that would not have some adversaries, one must not house the walnut, even plant, or transplant near the oak, not even place it in a trench where an oak has been planted before, because these two trees have a natural hatred for each other, & cannot grow together.*”

By the close of the 18th century new information began to be added. For

example, in Phillips' *Pomarium Britannicum* (220), in addition to mention of Pliny, it is stated that a well known London strawberry-grower, Mr. Keen, has noted that "*the walnut is so injurious to strawberry beds, that they seldom bear fruit in the neighbourhood of that tree.*" The harmful effect of the walnut was common knowledge in Europe and for example, appears in de Stendahl's novel of 1831, *Le Rouge et le Noir*: "*Each of these cursed walnuts, said M. de Rénal when his wife admired them, costs me the harvest of a demi-arpent, wheat cannot grow under its shade.*" According to Crozier (64), the secretary of the Central Horticultural Society of France wrote: "*Shrubs and underwood will generally thrive and flourish when planted under beech trees, but will not even live when planted under the shade of the walnut.*"

During the latter half of the 19th century it became apparent that American species, most notably the black walnut (*J. nigra*), also were injurious to other plants. This seems to be first recorded in the *Transactions of the Illinois State Horticultural Society*. Firstly, Galusha (101), in discussing that "*certain kinds of trees are poison to an orchard*", recorded that his neighbour, in planting a row of black walnut trees on one side of his apple orchard, found after 12 years that almost all the adjacent apple trees had died. In 1874, there was a lively discussion at the Illinois State Horticultural Society (193) and Mr. McWhorter and Mr. Douglas agreed that black walnut affected the palatability of grass for stock. Mr. Bryant added that he had witnessed black walnut killing apple trees within a radius of about 25 meters and he thought that walnut roots were in some way poisonous. However, others at the meeting were in disagreement and, when Dr. Schroeder commented that walnut leaves "*contain a great proportion of bitter stuff and they embitter the ground and make it sick*", he was confronted with laughter.

Remarkably similar comments appear elsewhere in the American agricultural press. A Pennsylvanian farmer, Mr. O. Snowberger, wrote to a Farmers' Club in New York (7): "*I feel satisfied that I have seen three apple trees destroyed by black walnuts and I believe they destroy grape vines. I judge it is the water dropping from the walnut leaves that does the work.*". In a discussion before the Wisconsin State Horticultural Society in 1881, Stickney and Hoy (281) concluded that "*the main reason why vegetation does not thrive under these trees [black walnut] is the poisonous character of the drip.*"

In 1883, an American report similar to that by Galusha (101) was published in an English forestry Journal (8): "*Some thirty years ago I planted an orchard of about 200 apple trees on one of my farms - open prairie. Having a lot of three to four-year old Walnut trees growing from seed, I planted a few rows of them on the north side as a windbreak. Both did well for some time, and now some of the walnut trees have reached a height of 40 feet. The first row of Apple trees has long since been*

killed out. The rest of the orchard is doing well; having a large crop of fruit during the past season and is generally fruitful. With my experience, I should as soon think of feeding poison to my stock as planting such trees near enough to Apple trees to subject the latter to their influence. My grove of Walnut trees is much admired by passers-by. This would seem to deprive arboricultural schemes of the romance with which they have been surrounded in theory."

However, despite the apparent widespread experience of the so-called "walnut toxicity", Crozier (64) dismissed all such claims as unsupported.

3. THE EFFECTS OF WALNUTS ON OTHER PLANTS

3.1 *Juglans nigra*

3.1.1 Effects on crop plants

I. Grape vine : In the early twentieth century, Hedrick (125) stated that grape vines were harmed by walnut trees. The injurious effects of walnut were known to Schreiner and Reed (264, 265) at the USDA Bureau of Soils, but were not investigated by them.

II. Tomato : The unfolding of the walnut story really begins in the 1920s, as both the symptomatology and chemistry of walnut toxicity were elucidated at the Virginia Agricultural Experiment Station. Cook (61), in a brief note, described the wilting of tomato plants as affected by *Juglans nigra*. Massey (185, 186) collated many observations of his colleagues on the effects of black walnut on tomato. The results from a spraying experiment were particularly striking (186): a set of small square plots of tomato plants happened to be bordered by two black walnut trees, all tomato plants within 15 m and 12 m respectively, of the two trees were injured. Massey noted that, in a large alfalfa field which contained a solitary black walnut tree, alfalfa was generally absent and replaced by grass within the vicinity of the tree and that the damage seemed root-related. Massey observed that black walnut injured tomato plants and potato plants, to a lesser extent, but not beets, snap beans or corn in his home garden. He subsequently set up three simple experiments. He established that walnut root bark added to water culture would cause wilting and browning of roots of tomato within 48 h, that root bark added to soil would also cause poor growth, but that walnut soil alone caused no effect. Massey concluded that there must be some toxic principle which may be initially insoluble in water, or may alter chemically once it leaves the root. He surmised that the chemical was likely the hydroquinone juglone.

III. Apple : Schneiderhan (258, 259, 260) reported the demise of apple trees which were near black walnut trees, apparently a commonly known problem in Virginia. He added that only *J. nigra* and *J. cinerea* appeared injurious, as *J. hindsii* and *J.*

californica supported intercrops; he also regarded *J. regia* as not injurious. In the course of a cursory survey in Frederick County, Virginia, Schneiderhan found eighteen instances of walnut injury to apple trees. The average distance of 48 dead apple trees was about 11.9 m from a walnut tree and the average distance of 14 injured apple trees was about 14.3 m. Schneiderhan speculated that the relatively common occurrence of walnut toxicity in Frederick County may be related to the shallow soil and consequent intermingling roots. He also speculated that among the local apple varieties, Stayman may be more resistant to walnut toxicity. Schneiderhan's observations were confirmed by the experiences of Smith (272) whose walnut trees were on various grafted stock. Smith also found that alfalfa suffered on his property. Difficulties with black walnut were also reported from West Virginia (210, 211).

In 1928 Davis, working at the Virginia Agricultural Experiment Station isolated juglone from both hulls and roots of black walnut (70). Juglone was administered to both tomato and potato plants by injection into the stem, causing severe effects. Both natural and synthetically prepared juglone caused similar effects. The apparent identification of the cause of walnut toxicity was considered sufficiently important to warrant mention in the *New York Times* (11) and to gain service as a sermonic metaphor (204).

The various reports on walnut toxicity which appeared in the 1920's caused some degree of panic in certain quarters, as farmers who had not experienced any problems with walnut trees immediately felt threatened. Miller (195) attempted to rebut Schneiderhan's comments in describing an old apple orchard containing walnut, in which injured or dead trees were not near walnut trees. An editorial in the *Washington Star* (9) ridiculed the idea that the walnut tree was toxic and in alarmist manner, attempted to blame any scientist [Schneiderhan] for any loss of walnut trees due to their felling. Others (28) compared the effect of walnut simply to that of any other large tree exerting a strong competitive effect. The confirmation of juglone in walnut toxicity then generated a vigorous controversy which was staged over several years largely at the annual meetings of the Northern Nut Growers Association. Scepticism about walnut toxicity was led by Greene (110, 111) who cited a number of reports by farmers claiming that plants grew admirably under their walnut trees. Hershey (130) was outraged at some of the discussions at the 1929 meeting of the Northern Nut Growers Association and responded with a facetious note blaming any plant injury on "intangible poisons" and there was a move to suppress negative information about black walnut (12).

During the 1930s and 1940s there were continued, largely anecdotal, reports concerning the effects of black walnut on other crops (175, 191, 223, 237, 238, 262, 271, 272, 284, 323) but often the information was contradictory. MacDaniels, who had a long association with the Northern Nut Growers Association, was evidently

spurred by the Association (69) and reported on some pot experiments in which tomato and alfalfa plants were planted in walnut soil but there appeared little evidence of inhibition (175). Walnut hulls placed around a grape vine seemed only to enhance growth. Tomato plants planted close to a black walnut tree showed little adverse effect until late in the season. This work was continued by Brown (43), who showed that alfalfa and tomato in contact with walnut root bark were retarded in germination and strongly inhibited in seedling growth. Tomato seedlings grown in nutrient solutions with added walnut root bark were significantly inhibited even when given full nutrients but, particularly, when nitrogen deficient. There was evidently conflict among walnut growers over the issue of walnut toxicity, particularly as California growers with plantations of *J. regia* on their own roots or on grafted stock could not offer any evidence supporting a toxic effects (175), and, in 1948, the USDA (300) attempted to defuse the situation through the extraordinary means of a press release reassuring the public of the harmless nature of walnut trees, in particular, to tomato.

Curiously, the first detailed experimental work on the effects of black walnut on tomato was conducted in Germany, by Bode (32: 279, 280). When tomato seedlings were grown in the nutrient solution supporting two year-old walnut seedlings, Bode could find no evidence of injury, concluding that root excretion of juglone was not a significant factor. This is not surprising in view of the limited solubility of juglone in water, but Bode was also unaware that juglone production may become more significant with maturation of the tree. He found that juglone reached the soil through leaf leachate, leaf litter and also through the litter created by male catkins.

The interaction which has attracted the most detailed study is the pronounced effect of walnut on tomato. Originally, this was described by Masscy (185) and Brooks (42) as a wilting phenomenon. Bode (32) observed marked epinasty of the leaves, premature yellowing of the leaves, shortened internodal growth and decreased lateral root formation. MacDaniels and Pinnow (176) reviewed knowledge concerning walnut toxicity and confirmed that black walnut caused damage to both tomato and peony plants, primarily through root contact. MacDaniels (172) detailed the symptomatology of tomato plants grown near black walnut. The first sign was wilting, sometimes in a single branch and especially during daytime. Some affected plants eventually produced new growth from the base. Examination of the stem tissue revealed discoloured zones, browning of the vascular tissue and the presence of xylem tyloses, which may explain the wilting. In almost all cases of wilted tomato plants, MacDaniels was able to find one or more walnut roots in contact with the tomato root ball. Further work (177) attempted to assess walnut damage to other Solanaceae plants, potato and capsicum (pepper). Potato plants did wilt, but to a much lesser extent than tomato and no tyloses were found; the capsicum plants showed no obvious effects.

Tomato plants are unusually sensitive to juglone: 10 ppm juglone can cause 50% reduction of seedling growth, whereas 100 ppm juglone is lethal (314). The interaction of walnut with tomato plants was also investigated by DePalma (74, 75), who used one-year old seedlings of *J. nigra* in glasshouse and field trials; however, the only inhibition recorded was when walnut root extract was applied to tomato plants and in field experiments, the tomato plants commonly showed enhanced growth when adjacent to walnut plants.

It has been reported that walnut may affect the taste of beets but not affect yield (221). The interaction of *J. nigra* with crops such as corn and bean planted in alley cropping systems has been demonstrated in trenching experiments (146, 147). While competition, particularly for water, is of prime importance in such systems, it appears that minimising the contact of crop roots with juglone is also significant. Kipkech (155) found that leaf vegetables varied in sensitivity to being alleycropped with *J. nigra*: the order of sensitivity was Swiss chard (*Beta vulgaris*) > kale (*Brassica oleracea*) > lettuce (*Lactuca sativa*) > parsley (*Petroselinum crispum*). Nutrients such as nitrogen, phosphorus and potassium were generally higher in plantation soil, evidently due to increased inputs of organic matter by walnut but, perhaps, compensated by diminished growth due to inhibition by walnut.

3.1.2. Effects on co-planted trees

Black walnut may establish poorly on sites which lack tree cover (49). The use of "nurse species", which either protect the young walnut trees from mechanical damage or, more importantly, enhance the soil conditions, has been recommended to accelerate and improve walnut growth (6, 46, 56, 73, 93, 98, 106, 213, 254, 305, 307). Much of this pioneering work was done at Forestry Science Laboratory, USDA North Central Experiment Station, Carbondale southern Illinois.

Nurse species may also decrease the growth of competing or allelopathic undergrowth species such as the *Festuca* grass (120, 243, 247, 306), notably *F. arundinacea*, itself an allelopathic species and reduce the incidence of walnut diseases such as *Microsphaerella* leaf spot and anthracnose (152, 153). Common nurse species are *Pinus* spp., *Robinia pseudoacacia*, *Eleagnus umbellata* and *Alnus glutinosa*. While pines are generally sensitive to juglone it may take ten years or so before the effects of juglone are apparent and, by this time, walnut trees are well established (6). The use of legumes such as black locust (*Robinia pseudoacacia*) has proved problematic as its rapid growth overtopped coplanted walnuts; lespedeza failed altogether (56). Riétveld (245) tested the effects of juglone (10^{-3} M to 10^{-6} M) on 14 herbs and shrubs potentially useful as covercrops or nurse species and found that all were sensitive to juglone. Germination and radicle extension were generally less affected than shoot elongation

and dry weight accumulation. The species most affected in bioassay were *Lonicera maackii*, *Lespedeza cuneata*, *Trifolium incarnatum*, *Alnus glutinosa* and *Eleagnus umbellata*. However, Ponder *et al.* (226) found that soil from walnut plantations, with and without *Alnus glutinosus* or *Elaeagnus umbellata*, had no significant effect on the growth or *Rhizobium* nodulation of the covercrop *Vicia villosa*, although inhibition could be demonstrated through application of juglone in sand culture.

Eleagnus umbellata and *Alnus glutinosa* are actinorrhizal and are capable of increasing soil nitrogen through the action of the actinomycete *Frankia*. However, it was found that nurse species may prosper for a period of 8-13 years, after which the increased root system of walnut and/or the apparent accumulation of juglone in the soil causes the decline of the nurse trees (246). Contrary to the findings above (245), juglone is reported to have little direct effect on *Alnus* growth but affects nodulation and the activity of *Frankia*. Curiously, of five *Frankia* isolates tested, the one associated with *Alnus crispa*, a species relatively rich in the phenolic pinosylvin, was the most resistant to juglone (311, 312). It was found that the growth of *Frankia in vitro* was reduced exponentially as juglone concentration increased from 10^{-6} M to 10^{-3} M (71). At a concentration of 10^{-4} M juglone had a severe effect on the growth, *in vitro*, of the nitrogen fixing symbionts *Frankia* and *Rhizobium* and concentrations as low as 10^{-6} M caused significant inhibition in *Rhizobium*, although *Rhizobium* was slightly more tolerant at juglone concentration of 10^{-4} M (72). In further experiments (205, 206), seedlings of *Alnus glutinosa* were grown hydroponically and it was found that juglone at concentrations of 2×10^{-5} and 2×10^{-6} M inhibited nitrogenase activity after one day and after five days, respectively. Juglone at 2×10^{-5} M caused reduced root respiration and plant growth. However, juglone added to soil only had an effect at a concentration of 10^{-3} M and this effect ceased after 22 days evidently due to detoxification by the soil. Contrary to the results of Fisher (89), the authors found that a wet soil regime did not increase the longevity of the juglone in the soil. Work by Heckman and Kluchinski (121) suggested that leaf litter of *J. nigra* did not contribute significantly to inhibition of nodulation or nitrogen fixation in legumes. Ponder and Tadros (227) examined the role of juglone in a 14-year old walnut plantation containing the nurse species *Alnus glutinosus* and *Eleagnus umbellatus* on an upland site in southern Illinois. They found that juglone levels, which were significantly greater in walnut-black alder plantings than in pure walnut or walnut-autumn olive plantings, could be the cause of the relatively early demise of black alder trees in walnut plantations. Ponder (225) also examined the interaction of black walnut with *Alnus glutinosa* and *Eleagnus umbellata* in a 15-year old bottomland plantation in southern Illinois and, similarly, found that lower concentrations of juglone in topsoil were associated with plantations coplanted with *E. umbellata*, likely due to enhanced microbial degradation. Ponder also reported that there were differences in the soil nitrifiers in different plantings. However, these differences were not directly correlated with juglone, but were likely caused through changes to the understorey vegetation.

Understanding the dynamics of juglone can be important in walnut plantation management, particularly where the trees are harvested for timber. The harvesting process can result in the release of substantial quantities of juglone in debris and through damaged roots (58). If it is desirable to maintain intercropped species, it may be preferable to harvest later in the year when juglone levels are low or, if replanted walnut seedlings require a competitive edge, then harvesting in summer may be advantageous. Often, the allelopathic effects of walnut are unforeseen; for example, Gabriel (100) describes how an arboretum for white birches (series *Excelsae*) was established on a site which was partly occupied by 12 surviving trees from a failed black walnut plantation. Within one year 15 out of 200 various white birches had died and of these, 13 were near a black walnut. Dead birches were replaced with new birch plantings and after 4 years, 11 of the 13 troubled walnut sites again caused birch mortality and a further 8 birches had succumbed near walnut trees, whereas there were only 4 other losses away from the walnuts.

The negative effect of black walnut on conifers planted nearby is well known and supported by numerous observations, where it has commonly been found that conifer plantations, especially those of *Pinus* spp., established next to walnut trees show high mortality near the common border (5, 42, 45, 87, 118, 218, 244, 262, 263, 321). Research with juglone has demonstrated that seedling growth of *Pinus strobus* can be inhibited by as little as 10⁻⁷ M juglone (51). Seedlings of *Pinus strobus* grown for 8-10 weeks in hydroponic culture were injured by 10⁻⁶ M juglone; *Larix leptolepis*, *Picea abies* and *Pinus sylvestris* by 10⁻⁵ M juglone; 10⁻⁴ M juglone killed *Larix leptolepis* and *Pinus sylvestris* and 10⁻³ M juglone killed all four species (97). Fisher (89) demonstrated that the allelopathic effect of black walnut on *Pinus resinosa* and *Pinus strobus* was linked with poor soil drainage and assumedly longer retention of juglone in the soil. Van Sambeek (303) concluded that walnut was a superior competitor on better sites and under competition stress, probably produced more juglone which affected pine; however, on deep well drained sites, co-existence was possible as juglone may not build up in the soil.

3.1.3. Effects on natural vegetation

Although *Juglans* spp. are considered to be amongst the best equipped plants to affect other plants via allelopathy, there are surprisingly few data on the effects of walnut on surrounding vegetation under natural conditions. However, it was not until 1951 that Brooks (42) attempted to document the effects of walnut on surrounding vegetation in a broad context, although most of the trees studied were in an agricultural setting. In view of these well known effects, Conrad (59) investigated the effect of leaf and hull extracts of black walnut on the germination and seedling growth of eight deciduous trees including black walnut itself, but found no significant effects.

The effects of fresh leaf and hull extracts on the early germination stages of *Liquidambar styraciflua*, *Platanus occidentalis* and *Robinia pseudoacacia* were examined more closely; but any inhibitory effect proved temporary. Bratton (38) examined the effects of *J. nigra* on old field succession and found that it was inhibitory to *Ulmus americana* and *Fraxinus pennsylvanica*. De Scisciolo *et al.* (77) compared the understorey vegetation in several planted mixed hardwood stands containing *J. nigra*, *Acer saccharum* and *Quercus rubra* and could detect no qualitative differences. The density of understorey vegetation was actually significantly higher under *J. nigra*. The only significant interactions recorded were positive associations with *Rubus occidentalis*, *Circaea quadrisulcata* and *Dryopteris spinulosa* and an unexpected negative interaction with *A. saccharum* seedlings. Recently, Talley *et al.* (288) found that the root-climbing liane *Rhus radicans* is less abundant than expected on *J. nigra* and that bark extract can inhibit the germination of *R. radicans*. The absence of the herb dittany (*Cunila origanoides*) under certain hardwood species led van Sambeek *et al.* (304) to investigate the effect of root, foliage and decaying leaves leachates of several species, including *J. nigra*; however, the authors could not find any significant effect attributable to allelopathy.

3.2. *Juglans regia*

3.2.1. Effects on other plants

The Persian walnut *Juglans regia* is widely grown throughout the world as an ornamental or crop tree. Its inhibitory effect on understory vegetation is supposedly "well known" (169), but has been little studied in comparison to black walnut. Molisch (197) found that volatiles from Persian walnut shoots were slightly inhibitory. However, most information regarding the Persian walnut seems anecdotal. During the early years of the black walnut controversy, California walnut growers noted poor growth of plants under *J. regia* but found that this could be remedied through nitrogen application (175). Generally, it is acceded by American growers agreed that *J. regia* is less toxic than *J. nigra*, although results (222) illustrate that the relative degree of inhibition of the two species in bioassay depends on the test species. It has been noted that potatoes, beans and alfalfa do not grow well beneath walnut (162). In northern India, *J. regia* is commonly grown along bunds and terrace risers of cultivated fields and there is low species richness underneath the canopy in comparison to control areas (24, 25). Furthermore, of eight trees studied, *J. regia* was found to have the most pronounced effect in reducing winter crop biomass (by 69%) and an even more pronounced effect on summer crops. Leaf leachates of *J. regia* were found to inhibit germination of several agricultural species (194) and leaf extracts of *J. regia* were inhibitory to seedling growth of wheat and corn and to germination of corn, but not wheat (294). Walnut has also been implicated in "soil sickness" problems, that is, the re-establishment or maintenance of a walnut plantation may prove difficult for no

obvious reason (92). While organic compounds have been identified in contributing to "soil sickness" problems of fruit species such as apple and peach, there are no such data about walnut, as yet, and it may be that temporary depletion of soil nitrogen by understory vegetation is the major cause.

Grümmer (114), in his important monograph on allelopathy, remarked that in its native habitat in Asia Minor, walnut woodland has a rather poor understory which may be linked in some way to juglone, but he offered no evidence. In recent times, this view has been confirmed by Hussain *et al.* (134) who further reported that, in Pakistan crops such as corn, turnip, potato and beans were commonly unthrifty when grown near walnut trees. The authors subsequently found that extracts of walnut leaves, stems, hulls and bark, litter leachate and rain leachate inhibited the germination and seedling growth of corn, turnip and bean. Shoot extracts of *J. regia* were found to completely inhibit the germination of winter weeds such as *Alopecurus myosuroides*, *Lactuca sativa* and *Raphanus raphanistrum*, while the grass *Lolium multiflorum* was not significantly affected (301). With summer herbs, *Amaranthus retroflexus*, *Digitaria sanguinalis*, *Portulaca oleracea* were significantly inhibited, while *Prosopis stephaniana* and *Xanthium strumarium* were not. In view of the potential effects of juglone, Bauckmann (22) sluitd four different mixtures of grasses under walnut trees, and found no effects of suppression.

Kolesnichenko (158) noted that oak was inhibited by walnut. Leaf leachates, root extracts and soil extracts of *J. regia* have all been shown to demonstrate some degree of inhibition in bioassay (23, 159, 249), but little else is given. Tyzh *et al.* (299) grew walnut seedlings in excavated walnut soil and found no injurious effects, which is not surprising in view of the lability of juglone in soil as reported with *J. nigra*.

3.2.2. Effects on phytoplankton

It has been suggested that walnuts may affect freshwater biota through runoff and/or the leaching of walnut litter in water; this may be a particular problem in areas supporting walnut processing where washings are feared to harm fish (232). While the effects of juglone on aquatic animals are well known, its effects on phytoplankton are comparatively little known. Juglone was found to affect *Spirogyra* and *Chilomonas* at concentrations as low as 10^{-7} M (102), and studies with *Euglena* showed that photosynthetic forms were far more sensitive than colourless forms (261). Krajci and Lynch (160) surveyed the inhibitory effects of walnut hull extracts and juglone on a number of microorganisms including the cyanobacteria *Calothrix*, *Anabaena* and *Anacystis* and the green algae *Bracteacoccus* and *Coelastrum*. However, concentrations of juglone were in excess of 30 ppm. Randall and Bragg (234) found that the cyanobacterium *Nostoc commune* and the desmid *Scenedesmus* were inhibited

by 1 ppm juglone and the cyanobacteria *Anabaena flos-aquae* by 0.5 ppm juglone, whereas *Chlorella pyrenoidosa* was unaffected even by 10 ppm juglone. At very low concentrations (10 ppb, 100 ppb), juglone had a slight stimulatory effect on *Nostoc*, *Anabaena* and *Scenedesmus*. Kessler (150, 151) found that the green algae *Closterium*, *Microsterias*, *Pandorina*, *Eudorina* and *Spirogyra* were even less sensitive to juglone as these species were either unaffected or showed slight stimulation at 1.74 ppm (10^{-5} M) juglone. He, thus, concluded that the most likely effect of walnut leachate on freshwater algae was increased biomass because of inhibition of herbivores more sensitive to juglone.

3.3. Other walnut spp.

I. *J. cineraria*: *J. cinerea*, another native of eastern North America, is known as the butternut, or less commonly as the white walnut. It is of little commercial value and is seldom planted, hence, it has not attracted attention similar to *J. nigra* and *J. regia*. Jones and Morse (145) reported early observations made by A.H. Gilbert that cinquefoil (*Potentilla fruticosa*), a common weed was generally found dead within a circular area often greater than the canopy of butternut (*Juglans cinerea*) trees and that injury seem related to intermingling of cinquefoil roots with butternut roots. The extent of the effect generally increased with the age of the tree. It has also been observed that *J. cinerea* was associated with the death of *Pinus mugo* (272). The only experimental work with *J. cinerea* showed no significant effects on tomato plants (74, 75), although the plants of *J. cinerea* were only a year old.

II. *J. major*: The Arizona walnut, *J. major*, is also regarded as an allelopathic candidate and *J. mandshurica* has been found to be inhibitory in bioassay (192).

The lack of convincing results demonstrating allelopathy with *J. nigra* or *J. regia* in a natural setting is not surprising and is similar to the situation found with *Eucalyptus*, another genus with a good chemical armoury (327, 328). The results summarised, above, conform with the theories of Rabotnov (230, 231), who suggested that allelopathy is unlikely to be obvious in natural environments where selection over millions of years has already filtered those species intolerant of the toxins concerned. Conversely, allelopathy is likely to be most dramatic in environments, especially those artificially created such as in agriculture, where species with little coevolutionary history are brought together.

4. JUGLONE

The allelopathic effects of the walnuts have been usually ascribed to the compound known as juglone, although this approach is likely overly simplistic. Indeed, there is a variety of other secondary metabolites in *Juglans*, which have been implicated in allelochemical interactions, including phenolic acids (41, 117, 134).

flavonoids (184, 277), amines (168), alkaloids (30), terpenes (19, 169) and of course, naphthalenyl derivatives. Juglone (5-hydroxy-1,4-naphthoquinone or 5-hydroxy-1,4-naphthalenedione) is one of the naphthoquinones, which occur infrequently and usually in small amounts in plants; however, juglone is an oddity in that occurs in relative abundance. It is of great interest to ecologists as it has been implicated in a wide array of allelochemical interactions, including allelopathy. Its generally ready availability, its relative ease of isolation or preparation and its predictable performance in bioassay have made it a common subject in allelopathic work, for example, in classroom experiments (143, 198, 274, 285, 322), theoretical and methodological studies in allelopathy (82, 269, 315, 317) and bioassay studies of the comparative toxicity of various organic compounds (242). Juglone has also been the subject of numerous postgraduate dissertations in the plant sciences (33, 35, 74, 76, 88, 150, 166, 238, 239, 268, 314). Juglone was first isolated in 1856, but named juglone in 1877 and became primarily of interest as a dyestuff (320). Juglone is an orangeish compound which sublimes at 155°C. It can be noticed when fresh bark is stripped from walnut roots or fresh fruit hulls are cut, as the tissue turns yellowish due to the formation of juglone. There is some dispute over the natural occurrence of juglone: Daugherty *et al.* (68) maintain that juglone is restricted to the Juglandaceae, although they only tested the Juglandaceae and closely related families. Juglone occurred in all seven species of *Juglans* examined and in some species of related genera such as *Carya*, *Platycarya*, *Pterocarya*, *Cyclocarya*. However, there are also reports of juglone occurring in genera of unrelated families: *Lomatia* (Proteaceae) (196), *Caesalpinia* (Caesalpiniaceae) (203) and *Astragalus* (Fabaceae) (179). It has also been reported as a metabolite of various fungi: *Penicillium diversum* var. *aureum* (96), a mutant form of *Verticillium dahliae* (283) and *Mycosphaerella fijiensis* (282).

Research by Dow Chemical Co. has, apparently, suggested that UV radiation is required for the biosynthesis of juglone, which may explain why some experiments with *J. nigra* in glasshouses, where most of the UV radiation was lost, yielded negative results (174). However, in direct conflict with this is a statement by Cline and Neely (57), who maintained that juglone concentrations are higher in glasshouse seedlings than in field grown specimens. Recent work by Renesse (238) indicates leaf extracts of *J. nigra* and *J. regia* become much more inhibitory after exposure to O₂ and full light, which suggests that photocatalysis is involved. Juglone can be biosynthesised through an apparent nexus of pathways which originate with *o*-succinylbenzoic acid (199), derived from the shikimic acid pathway (see Figure 1). Juglone is most abundant in the plant as a glycoside of α -hydrojuglone (1,4,5-trihydroxynaphthalene) which, following enzymatic hydrolysis to release the sugar, is readily oxidised to juglone under aerobic conditions. Juglone or its precursors may participate in the formation of more complex compounds including methylated forms (27), several juglone oligomers, including dimers, trimers and possibly, tetramers have been identified in tissues from *Juglans* spp., but their function is unknown (122, 131, 212).

The fact that freshly cut walnut hulls will turn firstly yellow with juglone and then turn black, after further oxidation, indicates that other compounds can be easily formed from juglone (113). The fate of juglone in the environment has recently been elucidated (see Figure 1) and degradation proceeds enzymatically via the action of the bacteria *Pseudomonas putida* J1 or J2 which, ultimately, forms 2-hydroxymuconate semialdehyde and pyruvate (202, 240, 241).

At one point juglone itself was thought not to occur naturally in plant tissue but was thought to be present only in the form of a glycoside of 1,4,5-trihydroxynaphthalene (α -hydrojuglone). It is now accepted that juglone, in addition to its precursors and by-products, can be found in plant tissues, although most often in small quantities. However, in some structures, such as in fruits of *J. regia*, there can be a distinct gradient of juglone and its concentration is greatest in the epicuticular wax, where its concentration has been recorded as constituting up to 29.8% of the wax (228). Similarly, Binder *et al.* (27) found that juglone and 5-hydroxy -4-oxo- α -tetralone or 2,3-dihydro-5-hydroxy-1,4-naphthalenedione (β -hydrojuglone) comprised 18.6% (18.2 ppm) and 3.3% (3.2 ppm) of the naphthoquinone compounds of peelings of unripe black walnut (*J. nigra*) fruits whereas, for the whole hull, these quantities changed to 26% and 56%, respectively. It is not known whether juglone concentration changes with the age of the tree; experiments with walnut seedlings have often shown little allelopathic activity (e.g. 304). However, even cotyledons of germinated walnut seeds contain the β -glucosidase required to convert hydrojuglone- β -glucopyranoside to the aglycone α -hydrojuglone which, under aerobic conditions, rapidly oxidises to the more stable juglone (83).

Pedersen (214) has shown that electron spin resonance spectroscopy is a rapid and simple technique for assaying juglone/hydrojuglone from small plant samples; he found that, in eight species of *Juglans* screened, the leaf concentrations were 1.4-2.9 mg/g DW basis, although the technique which detects *ortho*- and *para*-quinols, thus, measures 'total juglone'. Recently, Girzu *et al.* (105) have provided a method for the specific determination of juglone from fresh samples, using high-performance liquid chromatography. Girdling experiments suggest that juglone is produced in the leaves or other green tissues and then translocated via the phloem,(37). Prativiera *et al.* (229) found that the xylary sap of *J. regia* contained juglone and could cause grafting failure. The juglone concentration in the xylem sap of *J. regia* has been found sufficient to inhibit seedling growth in bioassay (229, 291).

4.1.Pests management

The raison d'être for juglone, like most similar secondary metabolites, is linked primarily to defence against a range of enemies including insects, nematodes, bacteria and fungi. Juglone is well established as a deterrent to insects (104, 108, 116, 144, 208, 235, 295, 318) and insects which feed on members of the Juglandaceae commonly

are less affected by juglone (295). As is often the case in the course of coevolution, a few insects which feed selectively on *Juglans* have exploited the toxicity of juglone: for example, the larvae of the chrysomelid beetle *Gastrolina depressa* secrete juglone to deter ant predators (189). The ready availability of juglone has attracted some interest in exploiting its properties as an insecticide (31, 250).

Juglone has been shown to play a role in disease resistance in scab caused by *Cladosporium caryigenum* (37, 80, 329), walnut blight caused by *Xanthomonas campestris* (52) and anthracnose caused by *Gnomonia leptostyla* (57), galls caused by *Phylloxera* spp. (124) and *Fusicladium effusum* (123). Juglone has been employed as a successful treatment against some fungal plant pathogens (275). It appears to offer the first line of defence against invasion as it is, for example, an effective inhibitor of conidia germination in *C. caryigenum* but has no effect on subsequent colony growth or sporulation (329). This accords with the unusually high concentration of juglone in the cuticle. There is considerable seasonal variation in juglone quantities in differing tissues and juglone is usually most abundant during the younger stages of the plant structure. For example, Borazjani *et al.* (37) reported that juglone attains its highest level in leaves in June and in nuts in September. Juglone also appears to act as a phytoalexin and is commonly found to be more abundant in damaged or infected tissues (80, 115, 124), although Hedin *et al.* (122) found that the amount of 'total juglone', including its precursors, does not increase in damaged tissues of pecan. Juglone has also been found to increase the activity of polyphlooxidase *in vitro* (29) and, thus, may also play an ancillary role in defense. The presence of juglone in root tissue may be linked to its nematocidal effects (91, 178). An enigmatic feature of *Juglans* spp. is that, despite the presence of juglone, most species appear to be capable of forming mycorrhizae, both endotrophic and ectotrophic (e.g. 49, 266), which suggests that the fungal associates have mechanisms capable of detoxifying or sequestering juglone. Marked intraspecific variation to vasicular-arbuscular colonisation within seedlings of *J. nigra* (81) support this view.

4.2. Germination and seedling growth

As juglone is a naphthoquinone it is very reactive in biological systems, which probably explains why it generally is not recorded in large amounts in healthy plant tissue. There are numerous studies which have demonstrated that juglone can inhibit germination and seedling or plant growth (88, 133, 267, 324) or accelerate senescence (53), including one which has attempted to assess the effect of substitution type and position within the naphthoquinones (276). Among the few commonly occurring naphthoquinones, plumbagin (2-methoxy-5-hydroxy-naphthoquinone), followed by juglone, are the most inhibitory. Generally, juglone can act readily in oxidation/reduction reactions and, as a reductant, may concomitantly create potentially harmful free radicals such as superoxide and hydroxide (267). Juglone can be used as an artificial electron acceptor in the Hill reaction (249, 289); it is a useful tool in cell

biology generally as an electron acceptor and as an inhibitor of numerous cell processes, especially those which rely on the movement of cations such as K^+ or Ca^{++} across membranes (90, 207, 308). Juglone has been found to disrupt the activities of mitochondria and chloroplasts. These effects and other may be due to its reaction with thiol groups (127, 128, 157, 170, 209, 216, 217, 219). Juglone appears to have the ability to interfere with the synthesis (S) phase of the cell division cycle which may be due, again, to its reactivity with thiol groups and may have potential as an anti-cancer drug (148). Juglone can affect basic plant processes such as cell division, cell elongation and root formation (60, 156), and it behaves as a typical plant growth substance in bioassay in having a greater effect on radicle growth than on hypocotyl growth (293). Its similarity to synthetic plant hormones, such as naphthalene acetic acid, suggests that it may act as a plant hormone under certain circumstances (1, 32, 60). More recently, juglone has been shown to promote root formation in walnut seedlings (140, 141).

5. VARIABILITY IN THE EFFECT OF WALNUT

Probably the most vexing issue regarding allelopathy in walnut is the variability of the effect. This occurs for several reasons: (a) marked differences in the abundance of juglone and associated naphthoquinones among and within the different walnut species, (b) distinct seasonal differences in the occurrence of naphthoquinones in walnut species, (c) distinct differences in the susceptibility of plant species to walnut allelopathy and (d) geographical differences in allelopathic effect of walnut due largely to light conditions, soil conditions and soil microbiology.

5.1. Interspecific and intraspecific variation

Juglone is regarded as a constituent of most, if not all, of the known walnut species, and has been confirmed (either as juglone or hydrojuglone) in *Juglans nigra*, *J. regia*, *J. cinerea*, *J. mandshurica*, *J. major*, *J. ailantifolia*, *J. x intermedia* var. *vilmoreana*, *J. stenocarpa*, *J. rupestris*, *J. cathayensis* as well as some species of the related Juglandaceae genera *Carya*, *Pterocarya*, etc. (68, 103, 214). Among *Juglans* spp. it is generally considered that the highest juglone concentrations are found in *J. nigra* and that this species has been observed to cause the most damage to other plant species. However, Matveev (192) in bioassays with *J. mandshurica*, *J. nigra* and *J. regia* found that aqueous foliar extracts of *J. mandshurica* were most inhibitory. It is worth noting that levels of juglone have been found in *Pterocarya* spp. comparable to those in *Juglans* spp. (214). Thus, this genus also warrants study as an allelopathic candidate.

While there has been considerable work on the seasonal variability of juglone in walnut (see below), but little work has been done on intraspecific variation. It has been realised that in the nut-growing industry this facet has great importance in

breeding programs as juglone levels, particularly in pecan, have been linked to resistance against various pathogens. Although it is evident that the effect of walnut on other vegetation can be quite variable (42, 244) the causes can be manifold. Among the few data on intraspecific variation in juglone in walnut, Lee and Campbell (167) found that the *J. nigra* cultivar 'Ohio' had significantly greater concentration of juglone in the hulls than did the cultivar 'Thomas' and an unnamed seedling, but the same cultivar had the lowest juglone levels in its foliage. Cline and Neely (57) reported unusually high juglone levels (11.2 mg/g leaf DW) in one particular tree amongst their samples. De Scisciolo *et al.* (77) found up to ten-fold variation of juglone concentrations in soil under several different walnut trees; however, while these occurred on different soils, there appeared no correlation with any soil parameter. Renesse (238) found that three different varieties of *J. regia* differed markedly in their performance in various bioassays. There may or may not be variation in juglone concentration within a single tree; Lee and Campbell (167) found no difference in juglone concentrations from samples collected from the upper and lower parts of a tree, whereas Coder (58) recorded significantly higher juglone levels in the lower parts of the leaf crown, possibly due to differences in photosynthesis or light-induced decay of metabolites.

Another little studied aspect of juglone variation in walnut relates to the age of the tree. It is commonly reported that toxicity problems, for example, with nurse crop species, are not apparent for several years and then there is a relatively rapid decline of the nurse trees. This situation may be related to a genuine physiological difference between young and adult walnut trees (32, 74, 75, 221), or is more likely an expression of a juglone threshold in soil being reached due to an increasing root system and juglone load. In one study (167), a two-year old black walnut seedling was found to have a juglone concentration of 7.73 ppm (DW basis) in its roots in September, which was six times the concentration found in the foliage.

5.2. Seasonal variation

Most investigators have found that the abundance of juglone in the species known to contain high levels of juglone, such as *J. nigra*, conform to the plant apparency theory; that, is allelochemicals occur in tissues during the periods when they are most vulnerable to herbivores and/or pathogens. This occurs, typically, during leaf opening and during fruit formation and is reflected in reported high levels of juglone in leaves in June/July and high levels in fruits in August -September. However, the months showing maxima can vary among cultivars (167). The overall situation is further complicated, as different investigators have measured the abundance of different compounds under the rubric of "juglone". As juglone is toxic, it is usually stored as the more benign α -hydrojuglone glycoside. Thus, some investigators seeking pure juglone in walnut tissue may obtain low values (e.g. 32, 66)

while other investigators have chosen to measure juglone 'potential' or 'total juglone' through successive extraction in an oxidising environment, which means that juglone precursors, such as α -hydroquinone, form juglone during the extraction process. For example, Borazjani *et al.* (36) found that juglone levels in *J. nigra* leaves averaged about 1.3 mg/g (fresh weight) during the growing season and peaked in June, which accords with the data of other workers (109, 122, 123). Whilst Coder (58) used the same methodology as the preceding workers, his data appear to be in error, as he reported leaf concentrations of potential juglone of about 0.1 mg/g (dry weight), which was about a hundred-fold difference. The link between juglone concentration and development of the structure is emphasised by results from Hedin *et al.* (123) who found that immature *J. nigra* leaves formed in the late growing season (September) had 1.15 mg/g (FW) compared to 0.045 mg/g in the more common older senescing leaves. Data from *J. regia* shoots show also a build-up of juglone during the growing season with a peak, firstly, in May and then again in July (292, 331).

As discussed previously, juglone is convertible with the hydrojuglones and capable of forming glycosides. Thus, part of the problem in assessing the abundance of juglone in walnut tissue is in determining what exact methods have been used for juglone extraction and measurement. A comparison of two reports from the same group illustrates the discrepancies in the literature: Carnat *et al.* (50) extracted dried leaves of *J. regia* and found no juglone, while Girzu *et al.* (105) extracted fresh (May) leaves of *J. regia* and recorded specifically juglone, using spectrometry, levels of about 0.5% (fresh weight basis), which would convert to about 5% (dry weight basis).

5.3. Variation in the effect of *Juglans nigra* on other plants

At first, concern about black walnut centred on its effects on apple, grapes, tomatoes, potatoes and alfalfa but, once the problem became linked to the chemical substance juglone, there became fear in some quarters that black walnut was a "poison tree" and may have to be eradicated from the landscape. In 1951, Brooks (32) finally tackled the problem of which plants were and were not affected by black walnut as, over the course of 12 years, he had surveyed the effects of some 300 mature trees on neighbouring vegetation in five different States. His data are somewhat difficult to interpret as he provides only simple frequencies of some 60 tree species, 35 shrubs and vines and 123 herbaceous species within and without the root spread of black walnut but Brooks does describe those species which he judges to be tolerant or intolerant of black walnut.

There have been numerous reports of the effects of black walnut and/or juglone on individual species but there have been no serious attempts to document the effect of black walnut on vegetation patterning. Effects sometimes defy common sense: toxicity may be more apparent several meters from the trunk, even outside the canopy, because the roots nearest the tree are too deep to make contact with other roots (221). Clearly,

there is wide variation in the response of plant species to walnut but there can also be intraspecific variation in tolerance of walnut compounds such as juglone (245). In recent years, a considerable volume of information has become available through agencies such as the American Horticultural Society, university extension services and nurseries; much of this has been disseminated in leaflet form and/or in electronic form via the Internet. While most of this information is unsubstantiated, much of it has been generated by experienced or professional growers. The various lists of plants recorded in this century as being affected or unaffected by black walnut are collated in Table 2. Reports sometimes contradict one another, for example, as in the case of persimmon and holly, perhaps because of intraspecific variation in the walnut trees observed, different cultivars used or, more likely, soil differences. Furthermore, assessment of sensitivity may vary because of differing methodology; a plant such as *Lonicera maackii* is very sensitive to juglone in bioassay or hydroponic culture (244) but may grow satisfactorily under field conditions. There are some groups such as the conifers (Pinophyta), Betulaceae, Ericaceae, Oleaceae, Rosaceae and Solanaceae, where there is a high percentage of plants reported as affected by black walnut. In most of these groups there is at least one member which appears to be resistant and, commonly, it is a species whose natural range coincides with that of *Juglans* spp. and/or *Carya* spp. For example, the conifers *Juniperus virginianus*, *Pinus virginiana* and *Tsuga canadensis*; *Rhododendron periclymenoides* in the Ericaceae; *Forsythia* spp. in the Oleaceae; *Crataegus* spp., *Cydonia oblonga*, *Malus coronaria*, *Prunus serotina* and *Rubus occidentalis* in the Rosaceae; and *Physalis* spp. in the Solanaceae, further lends support to the arguments of Rabotnov (230, 231) mentioned previously. At the specific level, it seems also that there are cultivars that are unusually resistant to the effects of black walnut.

Table 2. Species which are reported as affected or unaffected by *Juglans nigra*

Division/Family/Sp	Common name	Affected	Unaffected
EQUISETOPHYTA			
<i>Equisetum arvense</i>	Horsetail		16
PTEROPHYTA			
<i>Asplenium platyneuron</i>	Ebony spleenwort		16
<i>Athyrium</i> spp.			84, 221
<i>Athyrium asplenoides</i>	Lowland lady-fern		16
<i>Athyrium thelypteroides</i>	Silvery spleenwort		16
<i>Botrychium dissectum</i>	Dissection grape fern		16
<i>B. dissectum</i> var. <i>obliquum</i>	Common grape fern		16
<i>Bulbinopsis bulbosa</i>			221
<i>Demstaedtia punctiloba</i>	Hay-scented fern		16
<i>Dryopteris cristata</i>	Crested wood fern		14, 15, 251
<i>Dryopteris intermedia</i>	Intermediate shield fern		16
<i>Dryopteris marginalis</i>	Marginal shield fern		16, 95
<i>Dryopteris spinulosa</i>			77
<i>Matteuccia struthiopteris</i>	Ostrich fern		15, 84, 221
<i>Onoclea sensibilis</i>	Sensitive fern		14, 16, 84
<i>Osmunda cinnamomea</i>	Cinnamon fern		14, 15, 16, 95
<i>Polystichum</i> spp.			15, 221
<i>Polystichum acrostichoides</i>	Christmas fern		15, 84, 95
<i>Woodsia obtusa</i>	Obtuse Woodsia		16
LYCOPODOPHYTA			
<i>Lycopodium complanatum</i> var. <i>flabelliforme</i>			16
PINOPHYTA			
<i>Juniperus chinensis</i>			17
<i>Juniperus virginiana</i>	Red cedar		16, 17, 34, 67, 84, 176, 221, 270
<i>Larix kaempferi</i>	Japanese larch	16	
<i>Picea abies</i>	Norway spruce	16, 67	17
<i>Pinus densiflora</i>	Japanese red pine	261	
<i>Pinus jefferyi</i>	Jeffrey pine		16, 17
<i>Pinus mugo</i>	Swiss mountain pine	16	
<i>Pinus nigra</i>	Austrian pine	261	
<i>Pinus resinosa</i>	Red pine	5, 16, 34, 67, 89, 176, 221, 270	
<i>Pinus rigida</i>	Pitch pine	16	
<i>Pinus strobus</i>	White pine	16, 67, 89, 218, 221, 244	
<i>Pinus sylvestris</i>	Scotch pine	16, 67, 244	
<i>Pinus taeda</i>	Loblolly pine	16, 67	
<i>Pinus thundbergi</i>	Japanese black pine	261	
<i>Pinus virginiana</i>	Scrub pine		16
<i>Thuja occidentalis</i>	Arborvitae	16	16, 17

<i>Tsuga canadensis</i>	Canadian hemlock		14, 16, 17, 67, 84, 251
MAGNOLIOPHYTA			
LILOPSIDA			
AMARYLLIDACEAE			
<i>Galanthus nivalis</i>	Glory-of-the-snow		14, 15, 84, 95, 251
<i>Narcissus</i> spp.	Daffodil		67
<i>Narcissus</i> 'John Evelyn', 'Unsurpassable', 'King Alfred', 'Ice Follies' <i>et al.</i>	Daffodil	16	
<i>Narcissus</i> 'Cheerfulness', 'Yellow Cheerfulness', 'Geranium', 'Tete-a-tete', 'Sundial', 'February Gold'	Narcissus		246, 176, 221
ARACEAE			
<i>Arisaema triphyllum</i>	Jack-in-the-pulpit		15, 16, 67, 84, 95, 221
<i>Asarum europaeum</i>	Wild ginger		14, 15, 16, 84, 251
COMMELINACEAE			
<i>Commelina communis</i>	Virginia day flower		16
<i>Tradescantia virginiana</i>	Spiderwort		14, 15, 84, 251
CYPERACEAE			
<i>Carex</i> spp. Sedges		16	
DIOSCOREACEAE			
<i>Dioscorea villosa</i>	Wild yam		16
IRIDACEAE			
<i>Crocus</i> spp.	Crocus		14, 15, 16, 84, 95, 251
<i>Iris</i> spp.	Iris		16, 221
<i>Iris siberica</i>			14, 15, 84, 95
LILIACEAE			
<i>Allium cepa</i>	Onion		16, 67, 176, 221, 283
<i>Asparagus officinalis</i>	Asparagus	16, 270, 283	
<i>Chionodoxa lucilliae</i>	Glory-of-the-snow		15, 84, 251
<i>Colchicum</i> sp.	Autumn crocus	67, 176, 221	
<i>Convallaria majalis</i>	Lily-of-the-valley	223	
<i>Erythronium</i> spp.	Dog-tooth violet		15, 84, 95, 221
<i>Hemerocallis</i> spp.	Daylily		15, 16, 67, 84, 95, 251
<i>Hemerocallis fulva</i>	Daylily		14
<i>Hosta</i> spp.	Plantain lily	223	15, 84, 95, 221
<i>Hosta fortunei</i>	Plantain lily		14, 251
<i>Hosta lancifolia</i>	Plantain lily		14, 251
<i>Hosta marginata</i>	Plantain lily		14
<i>Hosta undulata</i>	Plantain lily		14

<i>Hyacinthoides</i> spp.	Spanish bluebell	251
<i>Hyacinthoides hispanicus</i>	Spanish bluebell	14, 15, 84
<i>Hyacinthus</i> x	Hyacinth	14
<i>Hyacinthus</i> 'City of Haarlem'	Hyacinth	84
<i>Hyacinthus orientalis</i>	Hyacinth	15, 251
<i>Linum</i> cvs	Lily	221
<i>Lilium</i> 'Enchantment', Asian hybrids	Lily	16
<i>Liriope</i> spp.		16, 67
<i>Muscari botryoides</i>	Grape hyacinth	14, 15, 16, 84, 95, 251
<i>Ophiopogon</i> spp	Mondo grass	84, 221
<i>Polygonatum</i> spp.	Solomon's seal	84
<i>Polygonatum commutatum</i>	Solomon's seal	14, 15, 221, 251
<i>Scilla siberica</i>	Siberian squill	15, 16, 84, 251
<i>Tricyrtis hirta</i>	Toad lily	15, 84, 221
<i>Trillium</i> spp.	Trillium	15, 16, 67, 221
<i>Trillium cernuum</i>	Nodding trillium	14, 84, 251
<i>Trillium grandiflorum</i>	White wake-robin	14, 84, 251
<i>Tulipa</i> sp.	Tulip	283
<i>Tulipa greigii</i> 'Toronto'	Tulip	84, 95
<i>Tulipa</i> x Darwin 'White Volcano', Cum Laude'	Tulip	14, 84, 95, 251
<i>Tulipa</i> x 'Merry Widow', 'West Point'	Tulip	16
<i>Tulipa</i> x 'Blue Parrot'	Parrot tulip	84
<i>Uvularia</i> spp.		221
<i>Uvularia grandiflora</i>	Big merrybells	14, 15, 84, 95, 251
<i>Uvularia perfoliata</i>	Bellwort	16
ORCHIDACEAE		
<i>Habenaria lacera</i>		16
<i>Spiranthes gracilis</i>	Slender ladies tresses	16
POACEAE		
<i>Agrostis alba</i>	Redtop	16, 34, 67, 174, 221
<i>Andropogon virginicus</i>		34, 273
<i>Arrhenatherum elatius</i>	Tall oatgrass	16, 34
<i>Avena</i> sp.	Oat	34
<i>Bromus</i> sp.	Brome grass	16, 34
<i>Dactylis glomeratus</i>	Orchardgrass	16, 34, 67, 174, 221
<i>Danthonia spicata</i>	Poverty grass	34, 176, 221
<i>Festuca elatior</i>	Fescue	34, 67
<i>Festuca</i>	Tall fescue	270
<i>Holcus lanatus</i>		34
<i>Holcus mollis</i> 'variegatus'	Velvet grass	16
<i>Lolium</i> sp.	Rye	34
<i>Muhlenbergia schreberi</i>	Nimblewill	16, 34
<i>Panicum clandestinum</i>	Deer tongue grass	16, 34
<i>Phleum pratense</i>	Timothy grass	16, 34, 67, 176
<i>Poa compressa</i>	Canada bluegrass	16
<i>Poa pratensis</i>	Kentucky bluegrass	16, 34, 67, 211, 221, 270

<i>Triticum aestivum</i>	Wheat		16, 34, 67
<i>Zea mays</i>	Corn	258	16, 34, 176, 221, 270, 283
SMILACEAE			
<i>Smilacina racemosa</i>	False spikenard		16
<i>Smilax</i> spp.	Greenbriar		16
MAGNOLIOPSIDA			
ACERACEAE			
<i>Acer</i> spp.	Maple		221
<i>Acer ginnala</i>	Ginnala maple	244	
<i>Acer negundo</i>	Box elder		16, 17
<i>Acer nigrum</i>	Black maple		16, 17
<i>Acer palmatum</i>	Japanese maple		14, 16, 84, 248, 251
<i>Acer palmatum</i> 'dissectum'	Japanese maple		16, 248
<i>Acer rubrum</i>	Red maple		16
<i>Acer saccharum</i>	Sugar maple	77	
<i>Acer saccharinum</i>	Silver maple	16, 67	
ANACARDIACEAE			
<i>Rhus canadensis</i>	Fragrant sumac	16	
<i>Rhus copalina</i>	Dwarf sumac		16
<i>Rhus glabra</i>	Smooth sumac		16
<i>Rhus hirta</i>	Staghorn sumac		16
<i>Rhus radicans</i>	Poison ivy	287	16, 34, 221
ANNONACEAE			
<i>Asimina triloba</i>	Papaw		16, 17
APIACEAE			
<i>Daucus carota</i>	Wild carrot		16, 34, 270, 283
<i>Myrrhis alpestris</i>	Sweet cicely		15
<i>Pastinaca sativa</i>	Parsnip		16, 174, 221, 283
APOCYNACEAE			
<i>Vinca minor</i>	Periwinkle		15, 221
AQUIFOLIACEAE			
<i>Ilex opaca</i>	American holly	16, 251	17
<i>Ilex verticillata</i>	Michigan holly	16	
ARALIACEAE			
<i>Aralia spinosa</i>	Hercules club	16	
ARISTOLOCHACEAE			
<i>Aristolochia macrophylla</i>	Pipe vine	16	
ASTERACEAE			
<i>Achillea millefolium</i>	Common yarrow		16, 34, 270
<i>Ambrosia</i> spp.	Ragweed		16, 34
<i>Antennaria</i> spp.	Pussy's toes		16

<i>Aster</i> spp.	Aster	16, 34, 84, 270
<i>Bidens</i> spp.	Beggar-ticks	16, 34
<i>Calendula officinalis</i>	Pot marigold	14, 84, 251
<i>Chicorium intybus</i>	Chicory	16
<i>Chrysanthemum</i> spp.	Shasta daisy	16
<i>Chrysanthemum</i> spp.	Chrysanthemum	270, 283
<i>Chrysanthemum leucanthemum</i>	Ox-eye daisy	14, 15, 248
<i>Chrysanthemum morifolium</i>	Chrysanthemum	16
<i>Cirsium</i> spp.	Thistle	16, 34
<i>Dendranthema</i> sp.		251
<i>Doronicum</i> spp.	Leopard's-bane	14, 15, 84, 251
<i>Elephantopus</i> spp.	Elephant's foot	16
<i>Erigeron annuus</i>	Daisy fleabane	16, 34
<i>Erigeron philadelphus</i>	Philadelphia fleabane	16
<i>Eupatorium coelastinum</i>	Mist-flower	16
<i>Eupatorium purpureum</i>	Joe-Pye weed	16
<i>Helennum</i> spp.	Sneezeweed	16
<i>Helianthus</i> spp.	Sunflower	16
<i>Helianthus tuberosum</i>	Jerusalem artichoke	14, 15, 251
<i>Hieracium</i> spp.	Hawkweed	16
<i>Hieracium auranticum</i>	Orange hawkweed	14, 15, 251
<i>Lactuca</i> spp.	Wild lettuce	16
<i>Ligularia</i> sp. 'Desdemona'		251
<i>Prenanthes</i> spp.	Rattlesnake-root	16
<i>Rudbeckia hirta</i>	Brown-eyed susan	16
<i>Senecio aureus</i>	Golden ragwort	16, 34
<i>Solidago</i> spp.	Goldenrod	16, 34
<i>Taraxacum</i> spp.	Dandelion	14, 16, 34, 270
<i>Vernonia</i> spp.	Ironweed	16, 34
<i>Zinnia</i> spp.	Zinnia	84, 270, 283

BALSAMINACEAE

<i>Impatiens</i> spp.	Jewelweed	16
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BEGONIACEAE

<i>Begonia</i> spp.	Begonia	14, 84, 270
<i>Begonia x sempervirens cultorum</i>	Begonia	251

BERBERIDACEAE

<i>Berberis canadensis</i>	American barberry	16
<i>Epimedium</i> spp.	Epimedium	84, 95, 221
<i>Podophyllum emodi</i>	Mayapple	221
<i>Podophyllum peltatum</i>	Mayapple	15, 16, 84, 95

BETULACEAE

<i>Alnus glutinosa</i>	European alder	67, 244
<i>Alnus nigosa</i>	Smooth alder	16
<i>Betula alba</i>	White birch	16, 100
<i>Betula lenta</i>	Sweet birch	16
<i>Betula hata</i>	Yellow birch	16
<i>Betula nigra</i>	River birch	16

<i>Betula nigra</i> 'Heritage'	River birch		16
<i>Carpinus caroliniana</i>	American hornbeam	16	
<i>Corylus americana</i>	Hazelnut		16
BIGNONIACEAE			
<i>Catalpa bignonioides</i>	Common catalpa		14, 16, 84, 248, 251
BORAGINACEAE			
<i>Myosotis</i> sp.	Forget-me-not	223	
<i>Myosotis alpestris</i>	Forget-me-not		15, 221
<i>Myosotis sylvatica</i>	Forget-me-not		84
<i>Pulmonaria</i> spp.	Lungwort		14, 16, 84, 251
BRASSICACEAE			
<i>Brassica</i> spp.	Mustard		16
<i>Brassica oleracea</i> var. <i>botrytis</i>	Cauliflower		283
<i>Brassica oleracea</i> var. <i>capitata</i>	Cabbage	16, 67, 84, 270	283
<i>Dentaria</i> spp.			
<i>Hesperis matronalis</i>	Toothwort		16 251
BUXACEAE			
<i>Pachysandra</i> spp.		16	
CAESALPINIACEAE			
<i>Cassia marilandica</i>	Wild senna		16
<i>Cassia nitida</i>	Wild sensitive plant		16
CAMPANULACEAE			
<i>Campamula americana</i>	Tall bellflower		16
<i>Campamula latifolia</i>	Bellflower		14, 15, 84, 251
CAPRIFOLIACEAE			
<i>Lonicera</i> spp.	Honeysuckles		221
<i>Lonicera</i> sp.	Red-bud honeysuckle		283
<i>Lonicera canadensis</i>	American fly-honeysuckle	16	
<i>Lonicera maackia</i>	Amur honeysuckle	244	16, 17, 67
<i>Lonicera tatarica</i>	Tatarian honeysuckle		14, 16, 17, 248, 251, 283
<i>Lonicera xylosteum</i>	European fly honeysuckle		16, 17
<i>Sambucus canadensis</i>	Common elderberry		16
<i>Viburnum</i> spp.	Viburnum	221	84, 221
<i>Viburnum acerifolium</i>	Maple-leaved viburnum		16
<i>Viburnum dentatum</i>	Arrow-wood	16	
<i>Viburnum lantana</i>	Wayfaring tree viburnum		16, 17
<i>Viburnum opulus</i>	European cranberry bush viburnum	16	
<i>Viburnum plicatum</i>	Double-file viburnum	16	
<i>Viburnum prunifolium</i>	Black haw		16
<i>Viburnum sieboldii</i>	Siebold viburnum	16, 176	
CARYOPHYLLACEAE			
<i>Cerastium scandens</i>	Mouse-ear chickweed		16
<i>Dianthus armeria</i>	Deptford pink		16
<i>Stellaria media</i>	Chickweed		14

CELASTRACEAE

<i>Celastrus scandens</i>	Climbing bittersweet		16
<i>Euonymus</i> spp.		221	
<i>Euonymus alatus</i>	Burning bush		176, 221
<i>Euonymus americanus</i>	Strawberry bush	16	
<i>Euonymus europea</i>	European spindletree		16, 17
<i>Euonymus hamiltoniana</i>	Yeddo euonymus		16, 17

CHENOPODIACEAE

<i>Beta vulgaris</i>	Sugar beet	16, 283	16, 34, 176, 221, 270, 283
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CLUSIACEAE

<i>Hypericum</i> spp.	St. John's wort		16
<i>Hypericum prolificum</i>	Shrubby St. John's wort		16

CONVOLVULACEAE

<i>Convolvulus arvensis</i>	Field bindweed		16
<i>Ipomoea tricolor</i>	Morning glory		251
<i>Ipomoea tricolor</i>	Morning glory		14, 84
'Heavenly Blue'			

CORNACEAE

<i>Cornus alternifolia</i>	Alternate-leaved dogwood		16
<i>Cornus amomum</i>	Silky dogwood	16	
<i>Cornus florida</i>	Flowering dogwood		16, 17

CRASSULACEAE

<i>Sedum acre</i>	Golden-carpet		14, 15, 84, 251
<i>Sedum spectabile</i>	Showy stonecrop		14, 84, 251
<i>Sedum ternatum</i>	Stonecrop		16

CUSCUTACEAE

<i>Cuscuta</i> spp.	Dodder		16
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EBENACEAE

<i>Diospyros virginiana</i>	Persimmon	16	107
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ELAEAGNACEAE

<i>Elaeagnus angustifolia</i>	Russian olive	16, 244	
<i>Elaeagnus umbellata</i>	Autumn olive	244	16

ERICACEAE

<i>Azalea</i> spp.	Azalea	16, 84, 176, 221, 270	
<i>Gaylussica</i> spp.	Huckleberry	16, 34	
<i>Kalmia latifolia</i>	Mountain laurel	16, 34, 84, 176, 221, 223, 270	
<i>Pieris</i> spp.	Pieris	84	
<i>Rhododendron</i> spp.	Rhododendron	16, 84, 176, 221, 270	
<i>Rhododendron catawbiense</i>		223	
<i>Rhododendron maximum</i>	Rhododendron	223	

<i>Rhododendron periclymenoides</i>	Pinxterbloom		14, 84, 248
<i>Rhododendron</i> x Exbury hybrid 'Balzac'	Rhododendron	84, 95, 248, 251	
<i>Rhododendron</i> x Knap Hill hybrid 'Gibraltar'	Rhododendron	84, 95, 248, 251	
<i>Vaccinium</i> spp.	Blueberry	16, 34, 176, 221, 270	
<i>Vaccinium corymbosum</i>	Highbush blueberry	16	

FABACEAE

<i>Baptisia australis</i>	Blue false indigo	16	
<i>Caragana arborescens</i>	Siberian peashrub	244	
<i>Cercis canadensis</i>	Redbud		16, 17, 84, 270
<i>Coronilla varia</i>	Hairy vetch	244	
<i>Desmodium</i> spp.	Tick trefoil		16
<i>Gleditsia triacanthos</i>	Honey locust		16
<i>Gleditsia triacanthos</i> f. <i>inermis</i>	Thornless honey locust		17
<i>Glycine max</i>	Soybean		16, 184
<i>Lespedeza</i> spp.	Lespedeza		16, 56
<i>Lespedeza cuneata</i>	Sericea lespedeza	244	
<i>Lespedeza stipulacea</i>	Korean lespedeza	244	
<i>Medicago</i> spp.		34	
<i>Medicago sativa</i>	Alfalfa	16, 67, 176, 211, 221	
<i>Melilotus</i> spp.	Sweet clover		16
<i>Phaseolus lunatus</i>	Lima bean		16, 67, 176, 221
<i>Phaseolus vulgaris</i>	Wax bean; snap bean		16, 67, 176, 221, 283
<i>Pisum sativum</i>	Pea	270	283
<i>Robinia pseudoacacia</i>	Black locust		16
<i>Trifolium hybridifolium</i>	Alsike clover		16
<i>Trifolium hybridum</i>		34	
<i>Trifolium incarnatum</i>	Crimson clover	16, 67, 244	
<i>Trifolium pratense</i>	Red clover		16, 34
<i>Trifolium repens</i>	White clover		16, 34, 221
<i>Trifolium</i> sp.	Hop clover		16
<i>Vicia faba</i>	Broad bean		34, 270
<i>Vicia villosa</i>	Hairy vetch		225

FAGACEAE

<i>Castanea dentata</i>	Chestnut	16	
<i>Castanea mollissima</i>	Chinese chestnut	119	
<i>Fagus grandifolia</i>	Beech		16
<i>Quercus</i> spp.	Oak		221
<i>Quercus alba</i>	White oak	244	16, 17
<i>Quercus borealis</i>	Red oak		16
<i>Quercus coccinea</i>	Scarlet oak	16	
<i>Quercus imbricaria</i>	Shingle oak		16, 17
<i>Quercus rubra</i>	Northern red oak		16, 17
<i>Quercus stellata</i>	Post oak	16	
<i>Quercus velutina</i>			16

FUMARIACEAE

<i>Dicentra cucullaria</i>	Dutchman's breeches		15
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GENTIANACEAE

<i>Gentiana</i> spp.	Gentian		84
<i>Gentiana asclepiadea</i>	Gentian		221
<i>Gentiana septemfida</i>	Gentian		15, 221

GERANIACEAE

<i>Geranium robertianum</i>	Herb robert		14, 15, 16, 84, 95, 251
<i>Geranium sanguineum</i>	Cranesbill		14, 15, 16, 84, 251

HAMMAMELIDACEAE

<i>Hammamelis virginiana</i>	Witch-hazel	16	
<i>Liquidambar styraciflua</i>	Sweetgum		16, 17

HIPPOCASTANEACEAE

<i>Aesculus glabra</i>	Ohio buckeye		16
<i>Aesculus octandra</i>	Sweet buckeye	16	

HYDROPHYLLACEAE

<i>Hydrophyllum virginianum</i>	Virginia waterleaf		14, 84, 251
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JUGLANDACEAE

<i>Carya</i> sp.	Hickory		16, 221
<i>Juglans cinerea</i>	White walnut	16	
<i>Juglans nigra</i>	Black walnut	95	

LAMIACEAE

<i>Ajuga reptans</i>	Bugleweed	223	14, 15, 84, 95, 251
<i>Coleus</i> spp.	Coleus		270
<i>Collinsoma canadensis</i>	Rich-weed		16
<i>Cunila organoides</i>	Dittany		303
<i>Glechoma hederacea</i>	Ground ivy		14
<i>Hedeoma pulegioides</i>	Pennyroyal		16
<i>Leonurus cardiaca</i>	Motherwort		16
<i>Mentha piperita</i>	Peppermint		16, 270
<i>Monarda</i> spp.	Beebalm		84
<i>Monarda didyma</i>	Beeblam		15
<i>Monarda fistulosa</i>	Wild bergamot		14, 16, 251
<i>Monarda punctata</i>	Horsemint		16
<i>Nepeta hederacea</i>	Gill-over-the-ground		16
<i>Prunella vulgaris</i>	Heal-all		16, 34
<i>Pycnanthemum</i> spp.	Mountain mint		16
<i>Salvia</i> spp.	Salvia		94, 173, 221
<i>Stachys byzantina</i>	Lambs' ears		14, 15, 84, 251
<i>Thymus serpyllum</i>		223	
<i>Thymus serpyllum lanuginosus</i>		223	
<i>Thymus serpyllum coccineus</i>		223	

LAURACEAE

<i>Lindera benzoin</i>	Spicebush		16, 17
<i>Sassafras varifolium</i>	Sassafras		16

LOBELIACEAE

<i>Lobelia inflata</i>	Indian tobacco		16, 34
<i>Lobelia siphilitica</i>	Great lobelia		16
<i>Lobelia spicata</i>	Spiked lobelia		16

LYTHRACEAE

<i>Cuphea petiolaris</i>	Clammy cuphea		16, 34
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MAGNOLIACEAE

<i>Liriodendron tulipifera</i>	Tulip tree	244	16
<i>Magnolia</i> spp.	Magnolia	221	
<i>Magnolia acuminata</i>	Cucumber tree	16	
<i>Magnolia soulangiana</i>	Saucer magnolia	16, 67, 176	

MALVACEAE

<i>Alcea rosea</i>	Hollyhock		14, 15, 84, 251
<i>Hibiscus</i> spp.	Hibiscus		251
<i>Hibiscus esculentus</i>	Okra	270	
<i>Hibiscus syriacus</i>	Rose-of-Sharon		14, 84
<i>Malva rotundifolia</i>	Common mallow		16

MENISPERMACEAE

<i>Menispermum canadense</i>	Moonseed		16
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MORACEAE

<i>Morus alba</i>	White mulberry		17
<i>Morus rubra</i>	Red mulberry	16	

NYSSACEAE

<i>Nyssa sylvatica</i>	Black gum		16
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OLEACEAE

<i>Chionanthus virginica</i>	Fringe-tree	16	
<i>Forsythia</i> spp.	Forsythia		16, 84, 176, 221, 251
<i>Forsythia suspensa</i>	Weeping forsythia		14
<i>Fraxinus americana</i>	White ash	16, 244	
<i>Fraxinus nigra</i>	Black ash	16	
<i>Ligustrum</i> sp.	Privet	16, 67	
<i>Syringa</i> spp.	Lilac	16, 84, 270, 283	221
<i>Syringa x persica</i>	Persian lilac	176, 221	
<i>Syringa vulgaris</i>	Common lilac	176, 221	

ONAGRACEAE

<i>Circaea quadrisulcata</i>			77
<i>Oenothera</i> spp.	Evening primrose		16
<i>Oenothera fruticosa</i>	Evening primrose		14, 15, 251

OXALIDACEAE

<i>Oxalis</i> spp.	Wood sorrel		16, 34
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<i>Oxalis corniculata</i>	Creeping lady's sorrel		14
PAEONIACEAE			
<i>Paeonia</i> spp.	Peony	16, 67, 84, 176, 221, 270	
PAPAVERACEAE			
<i>Sanguinaria canadensis</i>	Bloodroot		14, 15, 84, 251
PLANTAGINACEAE			
<i>Plantago major</i>	Common plantain		16
<i>Plantago lanceolatum</i>	English plantain		16
PLATANACEAE			
<i>Platanus occidentalis</i>	Sycamore		16, 17
PLUMBAGINACEAE			
<i>Armeria vulgaris</i> var. <i>lauchiana</i>	Thrift	223	
POLEMONIACEAE			
<i>Phlox paniculata</i>	Summer phlox		14, 15, 16, 84, 251, 283
<i>Polemonium reptans</i>	Jacob's ladder	223	14, 84, 95, 251
POLYGALACEAE			
<i>Polygala sanguinea</i>	Milkwort		16
POLYGONACEAE			
<i>Fagopyrum</i> sp.	Buckwheat		34
<i>Rumex</i> spp.	Dock		16
PORTULACACEAE			
<i>Claytonia</i> spp.	Spring beauty		16
<i>Claytonia virginica</i>	Spring beauty*		15
PRIMULACEAE			
<i>Cyclamen</i> spp.	Cyclamen		15, 221
<i>Primula</i> spp.	Primula		221
<i>Primula x polyantha</i>	Polyanthus primrose		14, 15, 84, 251
RANUNCULACEAE			
<i>Anemone</i> spp.	Thimbleweed		16
<i>Anemone apennina</i>		221	
<i>Anemone quinquefolia</i>	American wood anemone		15
<i>Aquilegia caerulea</i>	Colorado columbine	16	
<i>Aquilegia canadensis</i>	Wild columbine	16	
<i>Clematis</i> spp.	Clematis		14, 84, 251
<i>Clematis terniflora</i>	Sweet autumn clematis		16, 17
<i>Clematis virginiana</i>	Virgin's bower		16
<i>Eranthis hyemalis</i>	Winter aconite		14, 15, 84, 251
<i>Helleborus</i> spp.	Hellebore		84, 221
<i>Ranunculus</i> spp.	Crowfoot		16

<i>Ranunculus ficaria</i>	Pilewort	221
<i>Ranunculus repens</i>	Buttercup	223
<i>Thalictrum</i> sp.	Meadow rue	15, 221
RHAMNACEAE		
<i>Ceanothus americanus</i>	New Jersey tea	16
ROSACEAE		
<i>Amelanchier canadensis</i>	Serviceberry	16
<i>Aronia arbutifolia</i>	Red chokeberry	16
<i>Cotoneaster</i> sp.	Cotoneaster	84, 95
<i>Crataegus</i> spp.	Hawthorn	16
<i>Cydonia oblonga</i>	Quince	16, 270
<i>Geum</i> spp. <i>Avens</i>	16	
<i>Kerria japonica</i>	Kerria	16, 17
<i>Kerria japonica</i> 'Pleniflora'	Double-flower kerria	16
<i>Malus</i> spp.	Apples	16, 34, 84, 176, 210, 211, 221, 270
<i>Malus</i> sp. cv. 'Stayman'		191
<i>Malus</i> spp.	Crabapple	176, 191
<i>Malus coronaria</i>	American crab	67, 221
<i>Malus hopa</i>	Hopa crabapple	16, 67
<i>Physocarpus opulifolius</i>	Nine-bark	67, 176
<i>Potentilla canadensis</i>	Common cinquefoil	16
<i>Potentilla fruticosa</i>	Shrubby cinquefoil	16, 176, 221
<i>Prunus americana</i>	Wild plum	16
<i>Prunus avium</i>	Sweet cherry	283
<i>Prunus cerasus</i>	Sour cherry	270
<i>Prunus pennsylvanicum</i>	Fire cherry	16
<i>Prunus persica</i>	Peach	211, 221
<i>Prunus serotina</i>	Black cherry	191
<i>Prunus subhirtella</i>	Weeping Higan cherry	16, 17
<i>Prunus tomentosa</i>	Nanking cherry	16
<i>Prunus virginiana</i>	Choke cherry	16
<i>Pyracantha</i> sp.	Firethorn	16
<i>Pyrus communis</i>	Pear	84, 221
<i>Pyrus calleryana</i>	Callery pear	16
<i>Ribes</i> spp.	Currant	16
<i>Rosa</i> spp.	Wild rose	16, 176, 221
<i>Rosa chinensis</i>	Fairy rose	16
<i>Rosa minima</i>	Fairy rose	16
<i>Rubus</i> spp.	Blackberry	16, 34, 176, 221
<i>Rubus</i> spp.	Red raspberry	221
<i>Rubus occidentalis</i>	Black raspberry	16, 34, 77, 95, 176, 221, 270
<i>Rubus odoratus</i>	Purple flowering raspberry	16
<i>Rubus prociumbens</i>	Dewberry	251
RUBIACEAE		
<i>Galium</i> spp.	Bedstraw	16, 34
<i>Galium odoratum</i>	Sweet woodruff	14, 15, 251
RUTACEAE		

<i>Zanthoxylum americanum</i>	Prickly ash	16	
SALICACEAE			
<i>Populus</i> sp.	Poplar		17
<i>Salix nigra</i>	Black willow	16	
SAMBUCACEAE			
<i>Sambucus canadensis</i>	Common elderberry	16	
SAPINDACEAE			
<i>Koelreuteria paniculata</i>	Goldenrain-tree		16, 17
SAXIFRAGACEAE			
<i>Astilbe</i> spp.	False spiraea		14, 15, 84, 95, 251
<i>Heuchera</i> spp.	Coral bells	16	15, 16, 221
<i>Heuchera x brizoides</i>			
'Pluie de feu'	Coral bells		14, 84
<i>Hydrangea</i> sp.	Hydrangea	16, 283	
<i>Hydrangea arborescens</i>	Wild hydrangea		16, 84, 95
<i>Philadelphus</i> spp.	Mock orange		95, 221
SCROPHULARIACEAE			
<i>Verbascum blattaria</i>	Moth mullein		16
<i>Verbascum thapsus</i>	Common mullein		16
<i>Veronica filiformis</i>	Creeping veronica		14
<i>Veronica officinalis</i>	Common speedwell		16
SIMAROUBACEAE			
<i>Ailanthus glandulosa</i>	Tree of heaven		16
SOLANACEAE			
<i>Capsicum annuum</i>	Pepper	16, 84, 176, 221	
<i>Lycopersicon esculentum</i>	Tomato	16, 34, 84, 176, 221, 210, 211, 270, 283	
<i>Nicotiana tabacum</i>	Tobacco	67	
<i>Physalis</i> spp.	Ground cherry		16
<i>Solanum aviculare</i>	Nightshade		221
<i>Solanum melongena</i>	Eggplant	16	
<i>Solanum tuberosum</i>	Potato	16, 34, 84, 176, 210, 211, 270	
STAPHYLEACEAE			
<i>Staphylea trifolia</i>	Bladder nut	16	
STYRACACEAE			
<i>Halesia carolina</i>	Carolina silverbell		16, 17
THYMELEACEAE			
<i>Daphne mezereum</i>	Daphne		14, 84, 251

TILIACEAE			
<i>Tilia americana</i>	Basswood	16, 67	
<i>Tilia heterophylla</i>	White basswood	16	
<i>Tilia platyphyllos</i>	Bigleaf linden		16, 17
ULMACEAE			
<i>Celtis occidentalis</i>	Hackberry	67	16, 17
<i>Ulmus americana</i>	American elm		16
<i>Ulmus fulva</i>	Slippery elm	16	
URTICACEAE			
<i>Pilea pumila</i>	Clearweed		16
VIOLACEAE			
<i>Viola</i> spp.	Violet		
<i>Viola canadensis</i>	Canada violet		16, 34, 270
<i>Viola cornuta</i>	Horned violet		14, 15, 84, 251
<i>Viola sororia</i>	Woody blue violet		14, 15, 84, 251
<i>Viola x wittrockiana</i>	Pansy		14, 84, 251
			14, 84, 251, 283
VITACEAE			
<i>Pathenocissus quinquefolia</i>	Virginia creeper		14, 16, 34, 84, 176, 221, 251, 270
<i>Vitis</i> spp.	Wild grape		16, 34, 176, 221, 270
<i>Vitis vinifera</i>	Grape	125	

5.4. Soil effects

A central issue in assessing the importance of juglone in allelopathy has been its longevity and movement in the soil. Juglone can persist in the soil for more than a year following tree removal, particularly if the stump has not been killed (221). Fisher (89) investigated three 22-25 year-old mixed plantations of *J. nigra* and *Pinus strobus* and *P. resinosa* in southwestern Ontario, Canada. In each plantation, three soil types with different drainage were represented. Pines growing near walnut trees on the well drained Brant soil showed no effects; those on the imperfectly drained Tuscola soil showed markedly reduced growth and those on the poorly drained Colwood soil were all dead. Fisher made no attempt to assess juglone levels in these soils but conducted an experiment by adding a fixed amount of juglone to the Brant soil maintained as either "wet" or "dry" and monitored its concentration for 90 days using bioassay. The dry soil lost its phytotoxicity after 30 days and juglone was not detectable after 60 days, whereas the wet soil continued to inhibit seedling growth and harbour juglone through the entire 90 days. Determinations of juglone in the field by Ponder and Tadros (227) at an upland site in southern Illinois showed that there was a gradient of juglone concentration away from a walnut tree and downward in the soil, with a

maximal mean value of 3.95 $\mu\text{g/g}$ (about 2×10^{-5} M) soil in topsoil (0-8 cm). A comparison of mixed plantings of black walnut and autumn-olive (*Eleagnus umbellata*) with walnut and European black alder (*Alnus glutinosa*) on similar soils revealed a significantly different juglone regime, likely caused by differing microenvironmental and microbiological conditions (226, 227). Higher juglone levels in black alder mixed plantings were consistent with the earlier decline of this species compared to autumn-olive. It was also found that nodulation in *Eleagnus angustifolia* co-planted with *J. nigra* did not occur when planted on bottomland soils, whereas there was good nodulation in upland soil; whether this difference is related to differing juglone regimes in the soil was not studied (332). De Scisciolo *et al.* (77) investigated the seasonal variation of juglone in soil, finding that the pattern conformed with juglone levels generally reported in the plant parts, with peaks in spring and autumn.

An often forgotten fact is that the effect of walnut trees seems to develop with maturation of the trees and, thus, may not be a problem in young plantings. According to Rietveld (244), there is a build-up period of 12-25 years before the effects of juglone may be noticeable. It is frequently observed that walnut may be grown successfully in the company of a nurse species such as *Alnus glutinosa*, *Eleagnus umbellata* or even pine for several years before any damage is apparent (244).

Another little studied aspect is the effect of juglone on soil arthropods and soil formation in general: the soil under walnut is likely to be different from neighbouring soils because of juglone or other factors. Brooks (32), in his survey of black walnut sites, found that soil under walnut was uniformly more alkaline, with differences in pH of up to 0.7. Wood and bark particles from trees containing juglone, *Carya illinoensis*

and *Juglans nigra*, are reported to decompose much more slowly than those from other hardwood species (4) and earthworms have been recorded as being scarce in walnut areas (176). Summers and Lussenhop (286) found that cores of walnut soil, when removed beyond the influence of the walnut canopy, increased in both arthropod number and diversity. Moreover, the authors concluded that the greater amount of soil organic matter associated with walnut could be ascribed to the general retardation of decomposer organisms.

The fate of juglone in soil has been surprisingly little studied until recently. It has been suggested that juglone levels in soil may decline as juglone becomes incorporated into soil organic matter (188, 253), as juglone has been reported in degradation products of humic acids from under walnut (47), or sorbed onto colloidal particles (89). The suggestion has been supported in part by the findings showing the low recovery of juglone after it had been added to sterile soil (77). This would also explain short-term inhibition as found, for example, by Conrad (59). It has also been suggested that the seeming variability of *Juglans* allelopathy may, in part, be due to variation in the ability of neighbouring plants to take up and detoxify juglone from the soil (296).

Rettenmaier *et al.* (240), in Germany, first discovered in black walnut soil an aerobic, motile Gram-negative rod-bacterium, identified as *Pseudomonas putida* J1, capable of metabolising juglone; further work showed a second strain *P. putida* J2 was able to degrade juglone (202). Given a glucose source, they could convert juglone stepwise to 2-hydroxyruyconic acid. Schmidt (255) in the U.S. demonstrated that a bacterium, identified also as *Pseudomonas*, collected from walnut soil, was capable of rapidly metabolising juglone. His research suggested that, under aerobic conditions, juglone was unlikely to persist in soils at significant concentrations as the bacterium had a high affinity for juglone. This point is noteworthy as it indicates that measurements of soil juglone must be done more or less immediately to have any meaning, as extractable juglone levels can decline within a relatively short period of time (< 4 h) and can be reduced to <1% of original concentration within 43 h (77). Williamson and Weidenhamer (325) argued that, while *Pseudomonas* may be an effective sink for juglone, it should be remembered that the juglone production is continuous, and that plant roots also may act as juglone sinks and thus compete for soil juglone. Furthermore, they observed that the products of juglone degradation through *Pseudomonas* remain largely unknown, and these in themselves may be allelopathic. Schmidt (256) replied that, despite these uncertainties, there remains no clear evidence that juglone in soil causes allelopathic inhibition, a position which he recently restated (257).

Finally, another problem which confronts researchers is the mobility of juglone in soil. Almost all determinations of soil juglone have been performed through extraction of soil with chloroform. Experiments attempting to recover juglone (50-200

µg) added to 100 g soil demonstrated that rapid subsequent aqueous extraction 10 min later yielded less than 1% of the added juglone (77). Weidenhamer *et al.* (316) state that the solubility of juglone is 52 ppm or about 3.5 mM, which is certainly adequate to cause severe growth inhibition, but it would seem that juglone becomes preferentially adsorbed by soil particles or organic matter.

6. DISCUSSION

While the genus *Juglans* provides what are probably the most widely accepted examples of allelopathic plants, it must be concluded that there still is no unambiguous demonstration of its effect. In a previous paper (326), I have argued that there are six criteria required to demonstrate allelopathy: (A) a pattern of inhibition (or association) of one species with another, (B) the putative donor plant must produce biologically active substances, (C) the putative donor must have a mode of release of allelochemicals into the environment, (D) there must be a mode of allelochemical transport and/or accumulation in the environment, (E) the receiver plant must have some means of allelochemical uptake and (F) the observed symptoms and pattern of growth cannot be explained solely by physical or other biotic factors, such as competition or herbivory.

What is clear in the case of walnut is that there is well known (although not that well documented) interaction with several plant species. The species of walnut are known to contain substantial quantities of naphthoquinones, particularly active in the form of juglone, as well as other phenolic compounds. It is less clear how exactly juglone is released into the environment, although most accounts agree that it is released as a water-soluble glycoside of hydrojuglone, which is then hydrolysed and oxidised to form the active juglone. However, juglone is not particularly mobile in the soil and it appears that it is readily adsorbed by soil organic matter, nearby roots, or bacteria. It has also been argued that, as juglone is rapidly metabolised by soil bacteria, it is unlikely to ever reach concentrations in soil, and consequently in roots, sufficient to cause any appreciable effect. Despite attempts (e.g. 268), no one has as yet demonstrated that juglone is actually taken up by plant roots, although there are numerous glasshouse experiments which provide data on the effects of juglone on plant growth, particularly in aqueous culture.

There is certainly too much evidence to conclude that walnut has no chemical effect on neighbouring plants. However, it certainly remains for more and better work to be done. Many questions need to be answered through more critical work. For example, what is the effect of walnut in its natural environment? How great is intraspecific variation in juglone production? How does juglone enter a receptor

plant? Is there any correlation between juglone concentration in walnut tissue and in soil and receptor plant response? Will investment in juglone research lead to lead to tangible benefits in agriculture, forestry, pharmacy or other areas?

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* Entries followed with an asterisk have been sourced from the Internet.