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Allelopathic Plants. 19. Barley (*Hordeum vulgare* L)

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CONTENTS

ABSTRACT

Barley is integrated with other crops to inhibit weed growth, through allelopathic interactions. Effects of barley on growth of other crops, weeds and autotoxicity among cultivars result primarily from allelopathy mediated by allelochemicals released from plant components and/or exuded from living roots. A limited number of allelochemicals are identified that contributes to allelopathic effectiveness of barley. High allelopathic effectiveness of barley has resulted in its wide adoption as a cover crop in sustainable agricultural systems for weed management. The allelopathic effectiveness varies among the barley cultivars, hence, selection programmes might improve the allelopathic potential of new cultivars used for weed management. Allelochemicals in barley may be candidates for natural herbicides and innovative approaches for integrating barley cover cropping with other cultural practices to improve the sustainable or ecologically-based weed management.

Keywords: Allelochemicals, allelopathy, autotoxicity, barley, flavonoids, green manure, gramine, hordenine, *Hordeum vulgare,* phenolic acids.

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1. INTRODUCTION

Hordeum vulgare L. (barley) is one of three species of genus *Hordeum* belonging to the tribe Triticeae of Poaceae family (89). Its Cultivation as domestic food crop started in the beginning of agriculture 10,000 years ago (26,73). It has originated in the Fertile Crescent [Israel, Jordan, Syria and southern Turkey to Zagros Mountains in Iran (59,89)]. During the early development of agriculture, barley was a staple food in bread-making and in soup and porridge dishes, However later, it became a multi-purpose crop [livestock feed, malt for brewing alcoholic beverages, pasture for grazing livestock, hay and silage for feeding livestock] and as a cover crop in rotation with cash crops, to reduce soil erosion, improve soil tilth and suppress weeds. It is adapted to a broad range of ecological conditions but grows best in temperate climates of cool and moderately dry seasons (73). Its early maturity characteristic, due to a low heat unit requirement, allows barley to be successfully cultivated at high latitudes of Alaska, Scandinavian countries, Tibet and Ethiopia, where the summers are too cool or too short to grow other cereals (73). In the Northern Hemisphere, spring barley, the most widely grown type planted in regions above latitude 40°N from March through June, is the primary source of malt and food grain. Below latitude 40°N, winter types are planted from mid-September through October, which allows the crop to be used for both pasture and feed grain production or for hay and silage (72,73). The global area devoted to barley production is about 65 million ha with 75% of the area in Europe, North Africa and western and southwestern Asia; North America contributes to about 10% of the area (26).

2. GENERAL CHARACTERISTICS AND UTILIZATION

2.1. MORPHOLOGY

Barley is an annual herbaceous monocotyledonous grass. During germination the barley caryopsis develops seedling roots followed by emergence of a coleoptile through the soil surface (79). Seminal roots develop after germination, growing outward and downward, forming a fibrous, branched root system. Internodes developing between the coleoptile and the first leaf form the crown from which the adventitious, or nodal, roots develop to help anchor the plant. When the plant reaches the six-leaf growth stage, 10 to 17 roots may be present reaching a depth of 45 to 60 cm, depending on soil characteristics, moisture and nutrient availability and may attain a depth of >1 m at maturity (79). Stems are cylindrical consisting of hollow internodes separated by solid nodes (joints), which are the origins of the leaf sheaths and range from 70 cm for dwarf types to >150 cm in length (79). Multiple stems (tillers) developed per plant depends on stand density and cultivar genetics and may number from one to six stems. Tillering is important in determining yield potential and compensation for variable plant densities. The inflorescence of a barley plant is a spike (head or ear) at the top of the stem, consisting of either two or six rows of fertile spikelets, in which the mature caryopses develop (79).

2.2. UTILIZATION

Approximately 85% of current world barley grain production is used as livestock feed (26,73) followed by malt for brewing beer and certain whiskeys (26). Barley is used as a food in those regions where other cereal crops do not grow (50). Its other food uses are breakfast cereals, bread flour and pearled barley as a soup thickener.

Winter barley is a versatile on-farm crop as a source of ample fall and winter pasture for grazing livestock and of feed grain after harvest of mature crop. The straw remaining after barley grain harvest is used for feeding ruminant livestock as well as for bedding in stables and feedlots. Barley is well-suited for rotations with other crops, as a nurse crop for establishment of long-term stands of grasses or legume forages such as alfalfa (*Medicago sativa* L.) and as an overwintering cover crop for protection against soil erosion (72). Recent research demonstrated that barley intercropped with berseem or Egyptian clover (*Trifolium alexandrinum* L.) provided high quality forage with high protein content for feeding livestock (87). The effectiveness of barley as a cover crop for suppressing weed infestations (4, 13) and as an amendment to water impoundments to inhibit algae (29,95) is due to allelopathic effects.

3. ALLELOPATHIC RESEARCH

3.1. CROP PRODUCTION SYSTEMS

Allelopathy in barley may be manifested to other crops ("crop allelopathy") when grown in various management systems, as autotoxic effects among certain barley cultivars, or toward various weed species.

3.1.1. Crop rotation: A limited number of studies that demonstrate allelopathic effects of barley to other crops were based on field observations of poor growth of crops planted into soil previously planted to barley in a crop rotation scheme. Field studies in Canada found that flax (*Linum usitatissimum* L.) growth was inhibited when grown in soils containing barley crop residues (34). Small-seeded crops were particularly susceptible to allelopathy, demonstrated by field studies of spring and winter barley residues on the soil surface in which germination and growth of lettuce (*Lactuca sativa* L.), cabbage (*Brassica oleracea* L.) and tomato (*Lycopersicon esculentum* Mill.) were severely reduced (76,77). Poor growth of bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum durum* L.) observed when grown in a rotation sequence after winter barley in Tunisia was shown in laboratory assays to be due to seedling growth inhibition by residues of barley (10).

3.1.2. Crop mixture/intercropping: Indications for growth interference other than competition are reported when clover (*Trifolium* sp.) growth was reduced by >50% when inter-planted with barley under abundant soil water and nutrients (56). Seedlings of numerous barley cultivars from a large germplasm collection inhibited seedling growth of perennial ryegrass (*Lolium perenne* L.) when grown together in an agar bioassay (13). Aqueous extracts of vegetative residues of spring barley inhibited seedling root growth of alfalfa (*Medicago sativa* L.) and radish (*Raphanus sativa* L.) in laboratory assays (78). Aqueous extraction of vegetative residues to assay for allelopathy suggested that allelochemicals were directly released from plant tissues rather than as a result of decomposition (76). Using a hydroponics growth system and a 'siphoning' bioassay apparatus, Liu and Lovett (49) demonstrated that allelochemicals directly released from barley seeds and seedling roots delayed germination and severely inhibited seedling growth of white mustard (*Sinapsis alba* L.).

3.1.3. Autotoxicity: Autotoxicity is defined as poor growth of a crop planted into soils continuously planted to the same crop (78). This is observable as decreased germination or seedling development by water extracts of the same crop residues, suggesting an interspecific form of allelopathy (78,80). Certain winter barley cultivars were found to be autotoxic, first illustrated by the inhibition of coleoptile and radical growth of the sensitive barley cultivar 'Manel' by the allelopathic cultivar 'Rihane' (11). Barley plant components grown under adverse environmental conditions, especially drought stress, increased the severity of allelopathic effects in the autotoxic response (63). Allelochemicals involved in autotoxicity included a combination of phenolic acids, which varied seasonally in plant content depending on environmental conditions (64). The practical implications of the research on autotoxicity include recognition of barley as a high-allelopathic risk in barley-barley cropping sequences, especially in semi-arid regions, information useful in decision-making by producers when selecting barley cultivars for planting in cereal crop rotations.

3.1.4. Weed suppression: Suppression of weed growth by barley and other plants was noted over 2000 years ago; the relationship of weed suppression to chemical substances released from these crops and the first description of this process as allelopathy developed during the 1800's and early 1900's (2,75,96). Only within the last 45 years has the deliberate exploitation of allelopathy for weed management been intensively pursued. The use of "cover crops" (crops planted during phases when main crops are absent and fields are otherwise fallow) takes advantage of allelopathic properties to manage weeds without inputs of synthetic herbicides. Barley is particularly effective as a cover crop for use in weed management because it rapidly establishes under a wide range of soil and environmental conditions and quickly grows to shade out weeds in addition to releasing allelochemicals to suppress weed growth (16). Early studies of the effects of barley as a "smother crop" for suppressing weed growth found that substances released from the foliage contained allelopathic activity responsible for severely inhibiting growth of chickweed (*Stellaria media* L.) (66). Several laboratory or growth chamber studies have demonstrated allelopathic effects of extracts of barley plants on seed germination and seedling growth of numerous weed species (17,20,52,65). Although growth reduction of weedy *Brassica* species under irrigated field conditions was largely due to superior competitiveness of barley for light and nitrogen, allelopathy as a component of overall interference could not be excluded (47). In field studies under no-tillage, spring barley residues reduced weed densities by ≤90% compared with soils devoid of surface residues (77). Subsequent studies confirmed the effectiveness of barley residues in reducing plant densities of the weeds portulaca (*Portulaca oleracea* L.) and smooth crabgrass [*Digitaria ischaemum* (Schreb.) Muhl.] 60 days after killing the barley with paraquat (76). Barley residues added to the soil surface of field plots inhibited emergence of eastern black nightshade (*Solanum ptycanthum* Dun.) by 98% and yellow foxtail [*Setaria glauca* (L.) Beauv.] by 81% 30 days after planting the weed species (19). Barley grown in rotation with wheat provided an apparent residual weed control observed in the wheat crop for ≤ 2 years (46). The allelopathic potential of several barley cultivars was detected by wild mustard (*Sinapsis arvensis* L.), a sensitive test species for detecting germination and seedling growth inhibition differences among the cultivars (65).

3.2. AQUATIC SYSTEMS

Addition of barley straw to aquatic sites including lakes and waterways is a sustainable approach to reduce the growth of undesirable algae in water due to eutrophication. This allelopathic effect of barley against filamentous algae was observed in 1980, when rotting barley straw in a canal in England reduced the density of floating algae (95). Subsequent laboratory studies demonstrated that the inhibitory substances were released from the straw during leaching by water (29). This finding has implications for sustainable use of a natural product (barley straw) to control algae in sensitive aquatic systems, where herbicides use is not environmentally acceptable.

3.3. ALLELOCHEMICALS

Generally characterization of chemical constituents have focussed on effects on forage and feed quality, malting properties and insect and disease resistance, etc. Despite the widespread use of barley for weed suppression, little research has been conducted on the nature of allelochemicals in barley (6). Till now only 44 chemicals have been identified as potential allelochemicals that contribute to its allelopathic activity (Table 1).

Table 1. Allelochemicals identified in *Hordeum vulgare*

Compound	Plant component	References
A. Alkaloids		
Gramine (*N,N*-dimethylindolemethyl-amine)	Leaf, Root, Root exudate	35,36,40,50,100
Hordenine (*N,N*-dimethyltriamine)	Leaf, Root, Root exudate	40,50,53,56
B. Phenolic Acids, Phenolic Acid Derivatives		
(a) Phenolic acids		
Benzoic acid	Root exudate	2
Caffeic acid	Leaf, Seed, Stem, Root exudate	2,17,101
Chlorogenic acid	Leaf, Seed	41,101
m-Coumaric acid	Leaf, Stem	17
o-Coumaric acid	Leaf, Stem, Root exudate	2,17
p-Coumaric acid	Leaf, Seed, Stem, Root exudate	15,17,41,61,64,101
Coumarin	Leaf, Stem	17
Ferulic acid	Leaf, Seed, Stem, Root, Root exudate	2,5,41,51,61,64,101
Gentisic acid	Root exudate	2
Hydroxycinnamic acid	Leaf, Stem	17,51
p-Hydroxybenzoic acid	Leaf, Seed, Stem, Root, Root exudate	2,15,64,101
5-Hydroxyferulic acid	Leaf	61
Protocatechuic acid	Leaf, Seed	41,101
Salicylic acid	Leaf	41
Sinapic acid	Leaf	61
Syringic acid	Leaf, Seed, Stem, Root	64
Trans-cinnamic acid	Leaf, Root exudate	2,41
Vanillic acid	Leaf, Seed, Stem, Root, Root exudate	2,15,41,64,101

(b) Phenolic acid derivative		
Scopoletin	Root exudate	2
C. Flavonoids		
Apiginen	Leaf	38
Lutonarin	Leaf	51
Saponarin	Leaf	51
Cyanadin	Leaf	37
Isovitexin	Leaf	62
Lutonarin 3'-methyl ether	Leaf	82
Catechin	Seed	28
D. Cyanoglucosides		
Heterodendrin	Leaf	24
Epiheterodendrin	Leaf	24,60,74
Epidermin	Leaf	60,74
Sutherlandin	Leaf	60,74
Osmaronin	Leaf	60
Dihydroosmaronin	Leaf	60
3-ß-D-glucopyranosyloxy-3-methylbutyronitrile	Leaf	74
1-cyano-3-ß-D-glucopyranosyloxy-2-methylpropene	Leaf	74
4--D-glucopyranosyloxy-3-hydroxy-3-hydroxymethyl-butyronitrile	Leaf	74
E. Polyamines		
Hordatine A & B	Leaf	84
Putresceine	Leaf	92
Spermidine	Leaf	32,92
Spermine	Leaf	92
p-Coumaroylagmatine	Leaf	85
F. Hydroxamic Acids		
2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA) [1]	Leaf	3, 33

[1] Detected in wild *Hordeum* spp. only

3.3.1 Alkaloids hordenine and gramine: The alkaloids hordenine and gramine were reported 70 years ago (57,66). Although their wide biocidal activity against microorganisms and insects was known (18,98; Table 2), the phytotoxicity of gramine was not established until 1966 (66) and of hordenine until 1989 (53). Thereafter these alkaloids have since become the premier allelochemicals for explaining the allelopathic effects of barley (6). Demonstration of allelopathy using the purified compounds has been limited to

Table 2. Allelopathic interactions of barley with crops and pest organisms including weeds, insects, and phytopathogens

Target organism	Allelopathic effect(s)	Allelochemical factor(s)	References
Crop species			
Wheat (*Triticum* spp.)	Seedling growth inhibition; root growth inhibition	Phenolic acids; decomposition products	10,42,67,78
Barley (*Hordeum vulgare*)	Seedling growth inhibition; root growth inhibition	Phenolic acids	11,63,64
Sudangrass (*Sorghum* sp.)	Root growth inhibition	Decomposition products	67
Perennial ryegrass (*Lolium perenne*)	Seedling growth inhibition	ND	13
Alfalfa (*Medicago sativa*)	Seedling growth inhibition	ND	78
Red clover (*Trifolium pratense*)	Decreased vegetative growth	ND	56
Vetch (*Vicia* sp.)	Root growth inhibition	Decomposition products	67
Broadbean (*Vicia faba*)	Root growth inhibition	Decomposition products	67
Flax (*Linum usitatissimum*)	Decreased vegetative growth	ND	34
Cabbage (*Brassica oleracea*)	Germination inhibition	ND	76,77
Lettuce (*Lactuca sativa*)	Germination inhibition	ND	76,77
Radish (*Raphanus sativus*)	Seedling growth inhibition	ND	78
Broccoli (*Brassica oleracea*)	Root growth inhibition	Decomposition products	67
White mustard (*Brassica alba*)	Germination and seedling growth inhibition	Gramine, Hordenine	49
Tomato (*Solanum lycopersicon*)	Germination inhibition	ND	76,77
Weed species			
Barnyardgrass (*Echinochloa crus-galli*)	Germination and seedling growth inhibition	Phenolic acids	20,64
Bristly foxtail (*Setaria verticillata*)	Germination and seedling growth inhibition	Phenolic acids	20
Giant foxtail (*Setaria faberi*)	Seedling emergence and plant density reduction	ND	44
Yellow foxtail (*Setaria lutescens*)	Seedling emergence reduction	ND	19
Smooth crabgrass (*Digitaria ishaemum*)	Vegetative growth reduction	ND	76
Chickweed (*Stellaria media*)	Vegetative growth reduction	Gramine, Hordenine	66
Portulacca (*Portulaca oleracea*)	Vegetative growth reduction	ND	76
Black nightshade (*Solanum nigrum*)	Seedling emergence reduction	ND	19
Wild mustard (*Brassica kaber*)	Germination and seedling growth inhibition	Phenolic acids	65
Filamentous algae	Growth inhibition; reduced biomass density	Decomposition products	29,95
Insects			
Bird cherry-oat aphid (*Rhopalasiphum padi*)	Feeding acceptance deterrent	Volatile phytochemicals; Gramine DIBOA[1]	31,70,102 3
Greenbug (Schizaphis graminum	Reduced population density	Gramine	81,88,102
Grasshopper (*Camnulla pellucida*)	Feeding deterrent	Proteinase inhibitors	93

Phytopathogens			
Powdery mildew fungus (*Erysiphe graminis hordei*)	Spore germination inhibition; inhibition of leaf infection	Gramine	98
		p-coumaroyl-hydroxy agmatine	90
		Putresceine, Spermidine, Spermine	92
		Hordatine A & B	84
Foot rot fungus (*Helminthosporium sativum*)	Inhibition of leaf infection	Hordatine A & B	85
Brown rust fungus (*Puccinia hordei*)	Inhibition of leaf infection	Spermidine	32
Bacterial leaf blight (*Pseudomonas syringae*)	Decreased leaf infection	Gramine	83

ND: Not determined; [1] Observed in wild *Hordeum* spp. only

Table 3. Strategies for exploiting barley allelopathy in weed management

Strategy	Impact	References [1]
Crop rotation	Residual weed control for ≤ 2 years; minimize amount of herbicide used	46
Intercropping	Reduce weed infestations; improve soil quality	30
Cover cropping	Suppress weed infestations in subsequent cash crop; minimize amount of herbicide used	5,20
Cover cropping of barley + other allelopathic crops	Broaden spectrum of weeds suppressed	16
Crop rotation + cover cropping	Suppress weed infestations; minimize amount of herbicide used	48
Mulching; direct planting into mulch	Barley residues on soil surface inhibit weed germination/seedling growth in cash crop	48
Reduced tillage + cover cropping + crop rotation	Weed growth suppression; no herbicide inputs	8
No-tillage + barley residue from cover cropping	Weed growth and density reduced ≥ 90%	77
Cover cropping + crop rotation + bioherbicides	Increase weed suppression synergistically; reduce herbicide use	44
Inter-cropped barley killed with herbicide	Suppress late-emerging weeds in the cash crop	71
Inter-seeded cover crop + mycoherbicide	Improved control of target weeds i.e., bindweeds (*Convolvulus* spp.)	71
Combine highly competitive/allelopathic cultivars with bioherbicides	Increase weed suppression synergistically; reduce herbicide use	45
Enhance allelopathic activity through breeding	Improve effectiveness of barley used in crop rotation, cover cropping, mulching	94

[1] References cited are not a comprehensive bibliography but are intended to illustrate an integrated tactic.

indicator species of chickweed (66) and white mustard (49,50). Physiological effects of gramine and hordenine on susceptible plants include cell wall damage, increased cell vacuolation, damage to mitochondrial structure and disruption in cellular metabolism (50). When both alkaloids were combined and assayed on white mustard, the cellular damage increased, demonstrating a synergistic effect of gramine and hordenine. Gramine and hordenine concentrations in the barley plant vary among cultivars (35,36,40) and with environmental conditions [moisture, temperature and light intensity stresses (36)]. Increased allelochemical production due to exposure to environmental stress occurs in several plant species (22); thus, allelopathic effectiveness based on gramine and hordenine production of different barley cultivars grown under various environmental conditions may also be affected.

3.3.2. Phenolic compounds: Phenolic compounds contribute the greatest number of allelochemical compounds in barley, about 43%, all but one of which are phenolic acids. Phenolic acids occur widely in plants and influence many metabolic activities including the ability to modulate key cellular enzyme functions (101). Phenolic acids are also implicated in the expression of allelopathic activity by many plant species (4). In a survey of spring cereal crops varieties, Baghestani *et al.* (2) identified seven phenolic acids and one phenolic acid derivative (Table 1) released with root exudates of barley. Three phenolic compounds, (*o*-coumaric acid, vanillic acid and scopoletin) were more abundant in root exudates of "highly competitive" cultivars and were considered indicators of allelopathic potential and as contributors to overall competitiveness, traits that would be useful in breeding programmes for varietal selection. Bioassays of phenolic acids associated with barley foliage showed that salicylic acid, vanillic acid, p-coumaric acid, ferulic acid and chlorogenic acids possessed moderate to high allelopathic efficiency in growth inhibition of barnyardgrass [*Echinochloa crus-galli* (L.) P. Beauv.], suggesting a high potential for these compounds in herbicide development (41). Five phenolic acids (*p*-coumaric acid, ferulic acid, p-hydroxybenzoic acid, syringic acid, vanillic acid) were detected in several components of barley that contributed to autotoxicity (64). The barley variety and weather conditions during the growing season affected the concentrations of phenolic acids in plant parts (63,64). In bioassays, the combinations of phenolic acids often show synergistic effects (9,22), showing high overall allelopathic or autotoxic activity in those barley cultivars that produce numerous phenolic acids (2,64). Morphological and physiological effects of phenolic acids on susceptible plants are: reduced leaf expansion, leaf production, net carbon assimilation rate and stomatal conductance (68); decreased leaf water potential due to reduced osmotic potential and turgor pressure (23) and lower nutrient contents in roots and shoots (23).

3.3.3. Flavonoids: Flavonoids, phenylpropanoid compounds synthesized through the shikimate pathway (12,80), are widespread in plants and ecologically important as pigments, attractants, herbivore deterrents, and allelochemicals (37,80). Many biochemical investigations of barley reveal a rich source of flavonoids with biological activity, however, little is known about the function of these compounds, especially allelopathic activity. Because a limited number of flavonoids associated with other plants are directly involved in allelopathic interactions (12,55,80), flavonoids identified in barley are presented to indicate their potential contribution to overall allelopathiy of barley (Tables 1 and 2). In barley, unique flavonoids including lutonarin, saponarin and isovitexin are localized in the epidermis and mesophyll tissue of leaves and accumulate in response to exposure to high levels of ultraviolet (UV) radiation thereby protecting the plant from peroxidative damage (51,62). Recent research showing that UV-absorbing flavonoids in cotton (*Gossypium hirsutum* L.) leaf tissue contribute to a defense mechanism against the bacterial phytopathogen *Xanthomonas campestris* (21) suggests that a similar mechanism may function in barley. Other common flavonoids often implicated in allelopathic activity of many plants detected in barley include cyanidin (37) and catechin (28,55). The mechanisms of potential allelopathy by flavonoids include inhibition of germination and cell growth, disruption of adenosine triphosphate (ATP) formation, and interference with plant growth regulator (i.e., auxin) function (12).

3.3.4. Cyanogenic glycosides: The major form of cyanogenic glycosides found in barley is cyanoglucoside derived from the amino acid leucine and glucose (60). Hydrogen cyanide (HCN) may be released from cyanoglucosides and exert toxic effects toward other plants and pathogens; thus the presence of these compounds in barley suggests a potential allelopathic and pathogen defense system. Hydrogen cyanide is a potent inhibitor of electron transport in photosynthesis and respiration pathways (97). The release of HCN from barley leaf extracts has been observed, most likely derived from epiheterodendrin (27), however a linkage of HCN production with allelopathy was not demonstrated. Further complicating a defined role for cyanoglucosides was the observation that epidermin, epiheterodendrin and heterodendrin may be degraded by the phytopathogenic fungus *Erysiphe graminis* during infection and used as a carbohydrate source (74). Cyanoglucosides are sequestered away from enzymes necessary for degradation in a highly compartmentalized arrangement within the barley leaf; thus very limited amounts of HCN are released (27,60). Considerable additional research is necessary to determine the allelopathic potential of the cyanoglucosides present in barley.

3.3.5. Polyamines: The polyamines are compounds possessing two or more primary amino groups and found widely throughout the *Plantae* phylogenetic group (91). Polyamine concentrations in plants increase in response to various stress factors including drought, salinity, and pathogen infection (91). Concentrations of several polyamines including putrescine, spermine, spermidine, coumaroylagmatine, and hordetine in barley increase greatly when challenged with powdery mildew (91,92), brown rust (32), and foot rot fungal pathogens (85) and exhibit significant antifungal activity (Table 2). Polyamines tend to increase in leaf tissue surrounding the fungal infection to isolate the pathogen and suppress the spread of the disease (91). The impact of polyamines on weeds or insects has not been investigated.

3.3.6. Other compounds: The large number and diversity of plant-derived chemicals in nature suggests that many novel allelochemicals of barley remains to be discovered (96). For example, the detection of the hydroxamic acid DIBOA (Table 1) in wild *Hordeum* spp. (3,33) indicates the potential to discover it in domestic barley through screening of a global germplasm collection of barley cultivars. Numerous metabolites of barley have been described based on analyses for properties unrelated to allelopathy (i.e., malting) yet might be potential allelochemicals. For example, polyphenols detected in barley grain undergoing routine analyses for brewing quality (7), might contribute to allelopathy exhibited by barley seeds, which inhibited the growth of white mustard seedlings in bioassays (49).

3.4. RELEASE OF ALLELOCHEMICALS

An understanding of the modes of release of allelochemicals from the plant into the environment is important to develop effective cultural practices that exploit the allelopathic activity of crops as a successful weed management strategy (30,94). The primary modes of entry include exudation, leaching, decomposition and volatilization (1,52,80). In barley, gramine and hordenine are actively exuded from roots (beginning at the seedling growth stage and continues for at least 75 days); during this period the growth of competing weed species may be suppressed (52). Numerous phenolic acids are exuded through roots into the rhizosphere and adjacent soil, these are presumed to provide barley a competitive advantage over nearby growing plant species (2,15,86).

3.4.1. Allelochemicals in aqueous phase: Allelochemicals can be leached from the living plant during precipitation (rainfall, snow, dew, mist etc.) (100) and mulching of fresh residues on the soil surface or incorporated into soil, as evident from the detection of numerous compounds in water extracts from all parts of barley plant (15,17,52,64). The release of water-soluble allelochemicals from vegetative components is thought to be the primary factor contributing to the overall weed suppressive effect of barley used as a cover crop, mulch, or "smother crop" in crop production systems (17,20,66,76). In allelopathic mulch of barley residues, allelochemicals are most concentrated near the soil surface creating an "allelopathic zone" in which germination and/or seedling growth of small-seeded weeds are suppressed (48). Substances that may be allelopathic include those released during decomposition of fresh barley plant residues or mature straw directly into soil or aquatic ecosystems (30,52,95). The complexity of soil environment and the resident microbial community confounds the detection of specific decomposition products responsible for allelopathic effects of incorporated barley residues (6,52), although several organic acids formed during the decomposition under high soil moisture are often implicated in phytotoxicity to seedlings (52,54).

3.4.2. Allelochemicals in vapor phase: Release of volatile phytochemicals from intact barley plants at the V2 growth staged depressed the feeding preference of aphids (*Rhopalosiphum padi*) on adjacent barley host plants, suggesting that plants facilitate a biochemical signaling system to induce defence mechanisms prior to attack by plant herbivores (31,70). These findings suggest an interesting potential of barley for weed suppression in all barely growing regions. Indeed Belz (6) suggests that certain barley varieties might be selected with the ability to sense the competitive weeds and signal neighboring barley plants through volatile or rhizosphere compounds to induce biosynthesis of allelochemicals to suppress such invading weeds. Such biotic induction exists in rice (*Oryza sativa* L.) toward barnyard grass and sorghum [*Sorghum bicolor* (L.) Moench] toward velvetleaf (*Abutilon theophrasti* Medik.) (6). Volatile substances may not only affect the weeds growing in barley crop, but may also suppress the weed seedlings immediately after the soil incorporation of residues.

4. FUTURE DEVELOPMENTS

Although a limited number of allelochemicals have been characterized for barley, future efforts to exploit the allelopathic properties of barley in weed management may involve basic research on allelochemical structure and mode of action needed for potential herbicide development; selection and breeding programmes for optimum allelopathic activity and integration of barley allelopathy with other weed control methods. Allelopathic suppression of weeds and other pests using crops such as barley may be most effective as a component in a multi-faceted management system rather than as a single tactic approach (39). Potential strategies for exploiting barley allelopathy in weed management are presented in Table 3.

4.1. NATURAL HERBICIDE DEVELOPMENT

Continued isolation and identification of compounds implicated in allelopathy has been emphasized as a major research effort to develop natural herbicides or growth regulators that may possess novel modes of action and therefore, may more be effective than many current herbicides to which weeds have developed resistance (75,96). A precedent use of barley allelochemicals in pest management was suggested for gramine application to cereal crop foliage to control powdery mildew (98). It is also critical to consider the total complex of allelochemicals in the barley plant due to synergistic effects on weed growth (22,41). Information on allelochemical concentrations and combinations is necessary for the potential development of effective natural chemical-based herbicides.

4.2. SELECTION AND BREEDING FOR ALLELOPATHY

The wild populations, accessions and cultivars of crops differ in allelopathic traits and in the related resistance to pests. Weih (94) suggests that allelopathic activity is particularly high in cereal crops and should be used as an effective selection criterion in breeding programmes to enhance the competitive ability. Wild accessions and older cultivars of barley are more resistant to weed interference, traits that may have unintentionally been lost during selection of many modern cultivars (2,4,13,40,52). Potential for selection of allelopathic traits in barley is demonstrated in a study reporting that allelopathic activity of several barley cultivars was responsible for 7 - 58% of the observed weed suppressive effects (14). A subsequent study identified the barley cultivar ‘Athinaida’ as most allelopathic cereal crops to suppress the growth of barnyardgrass and bristly foxtail [*Setaria verticillata* (L.) P. Beauv.] and increasing the grain and silage yields of maize (*Zea mays* L.) planted into the barley mulch (17). A few examples from other cereal crops demonstrate the potential for selection of “allelopathic germplasm.” Evaluation of 3000 accessions of oat (*Avena sativa* L.) germplasm, found 25 accessions with significantly higher scopoletin than the standard cultivar ‘Garry’ (25). A rye (*Secale cereale* L.) cultivar, ‘Forrajero-Baer’, was selected for high production of hydroxamic acids in root exudates, which reduced weed growth in the field by 83 and 76% compared to wheat or oats, respectively (69). Use of barley wild types as sources of allelopathic potential may be necessary because these plants are evolved in the allelopathic and competitive environments of other plant species (75). Because allelochemical production in a plant is believed to be under genetic control, a breeding programme could be initiated to transfer allelopathic genes into modern cultivars to enhance the allelopathic activity (4,6,99). Alternatively, genes encoding for allelopathic traits from other plant sources could be inserted into barley as well as other major crops using genetic modification techniques (6,96) including development of transgenic cultivars with allelopathic traits (5). A need exists for cultivars with consistent performance in expressing allelopathy especially in sustainable agricultural systems and in environmentally-sensitive areas, where herbicides are restricted or banned (13).

4.3. INTEGRATED SUSTAINABLE WEED MANAGEMENT

Integrated sustainable weed management rely on many available strategies (Table 3) to reduce weed seed banks, prevent weed emergence and minimize the competition of weeds with growing crop (1). Integrating barley into a crop rotation sequence provided 'residual effects' in soil, likely due to release and persistence of allelochemicals, that reduced weed infestations in subsequent wheat crops grown during the following two years (46). Cover crops including barley will remain important components in ecological or biological weed management, which involves the use of various biological approaches including allelopathy, bioherbicides, crop competition and other cultural practices such as reduced tillage to obtain dramatic reductions in weed infestations similar to those that may be realized with herbicides (8,45). Barley included in combinations with other grass and legume cover crop species contributes to a wider range of allelochemicals released into soil and thereby broadens the spectrum of weed control (16). Barley seed inoculated with bacterial bioherbicide preparations delivered the bioherbicidal bacteria into soil at planting which allowed colonization of developing weed seedling roots and eventual weed growth inhibition (44). The combined effects of the bacterial bioherbicide and allelopathy of barley plant residues suppressed the growth of numerous weeds. Barley combined with *Vicia faba* L. reduced the weed biomass production by 47 – 85% more than with pure stands of either crop species (30). Also, a systems approach where an inter-seeded cover crop with a row crop is treated with a post-emergence bioherbicide to control emerging weeds (71) could be developed specifically for barley as the cover crop. Successful sustainable weed management based in part on inclusion of barley for allelopathic effects are in place (16,19) and serve as a foundation of experience and knowledge for integrating barley and eventually allelochemicals originating from the barley plant, on a broader scale in various cropping and horticultural systems.

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5. REFERENCES

1. Aldrich, R.J. and Kremer, R.J. (1997). *Principles in Weed Management*, 2nd Ed. Iowa State University Press, Ames, IA. 455 pp.
2. Baghestani, A., Lemieux, C., Leroux, G.D., Baziramakenga, R. and Simard, R.R. (1999). Determination of allelochemicals in spring cereal cultivars of different competitiveness. *Weed Science* **47**: 498-504.

3. Barria, B.N., Copaja, S.V. and Niemeyer, H.M. (1992). Occurrence of DIBOA in wild *Hordeum* species and its relation to aphid resistance. *Phytochemistry* **31**: 89-91.
4. Batish, D.R., Singh, H.P., Kohli, R.K. and Kaur, S. (2001). Crop allelopathy and its role in ecological agriculture. *Journal of Crop Production* **4**: 121-161.
5. Batish, D.R., Singh, H.P., Kohli, R.K. and Dawra, G.P. (2006). Potential of allelopathy and allelochemicals for weed management. In: *Handbook of Sustainable Weed Management* (Ed., H.P. Singh, D.R. Batish and R.K. Kohli), pp. 209-256. Food Products Press, Binghamton, NY.
6. Belz, R.G. (2007). Allelopathy in crop/weed interactions – an update. *Pest Management Science* **63**: 308-326.
7. Bendelow, V.M. (1978). Automated procedure for the estimation of total polyphenol content in beer, wort, malt and barley. *American Society of Brewing Chemists Journal* **35**: 150-152.
8. Bender, J. (1994). *Future Harvest – Pesticide-free Farming*. University of Nebraska Press, Lincoln, NE. 159 pp.
9. Ben-Hammouda, M., Kremer, R.J., Minor, H.C. and Sarwar, M. (1995). A chemical basis for differential allelopathic potential of sorghum hybrids on wheat. *Journal of Chemical Ecology* **21**: 775-786.
10. Ben-Hammouda, M., Ghorbal, H., Kremer, R.J. and Oueslati, O. (2001). Allelopathic effects of barley extracts on germination and seedling growth of bread and durum wheat. *Agronomie* **21**: 65-71.
11. Ben-Hammouda, M., Ghorbal, H., Kremer, R.J. and Oueslati, O. (2002). Autotoxicity of barley. *Journal of Plant Nutrition* **25**: 1155-1161.
12. Berhow, M.A. and Vaughn, S.R. (1999). Higher plant flavonoids: biosynthesis and chemical ecology. In: *Principles and Practices in Plant Ecology – Allelochemical Interactions* (Eds., Inderjit, K.M.M. Dakshini, and C.L. Foy), pp. 423-438. CRC Press, Boca Raton, FL.
13. Bertholdsson, N-O. (2004). Variation in allelopathic activity over 100 years of barley selection and breeding. *Weed Research* **44**: 78-86.
14. Bertholdsson, N-O. (2005). Early vigour and allelopathy – Two useful traits for enhanced barley and wheat competitiveness against weeds. *Weed Research* **45**: 94-102.
15. Börner, H. (1960). Liberation of organic substances from higher plants and their role in the soil sickness problem. *The Botanical Review* **26**: 393-424.
16. Bowman, G., Shirley, C. and Cramer, C. (1998). *Managing Cover Crops Profitably*. 2nd Ed. Sustainable Agriculture Publications, Burlington, VT. 212 pp.
17. Chon, S.-U. and Kim, Y.-M. (2004). Herbicidal potential and quantification of suspected allelochemicals from four grass crop extracts. *Journal of Agronomy and Crop Science* **190**: 145-150.
18. Corcuera, L.J. (1993). Biochemical basis for the resistance of barley to aphids. *Phytochemistry* **33**: 741-747.
19. Creamer, N.G., Bennett, M.A., Stinner, B.R., Cardina, J. and Regnier, E.E. (1996). Mechanisms of weed suppression in cover crop-based production systems. *HortScience* **31**: 410-413.
20. Dhima, K.V., Vasilakoglou, I.B., Eleftherohorinos, I.G. and Lithourgidis, A.S. (2006). Allelopathic potential of winter cereals and their cover crop mulch effect on grass weed suppression and corn development. *Crop Science* **46**: 345-352.
21. Edwards, W.R., Hall, J.A., Rowlan, A.R., Schneider-Barfield, T., Sun, T.J., Patil, M.S., Pierce, M.L., Fulcher, R.G., Bell, A.A. and Essenberg, M. (2008). Light filtering by epidermal flavonoids during the resistant response of cotton to *Xanthomonas* protects leaf tissue from light-dependent phytoalexin activity. *Phytochemistry* **69**: 2320-2328.
22. Einhellig, F.A. (1996). Interactions involving allelopathy in cropping systems. *Agronomy Journal* **88**: 886-893.
23. Einhellig, F.A., Muth, M.S. and Schon, M.K. (1985). Effects of allelochemicals on plant-water relationships. In: *The Chemistry of Allelopathy* (Ed., A.C. Thompson), *ACS Symposium Series* **268:** 179-195. American Chemical Society, Washington, DC.
24. Erb, N., Zinsmeister, H.D., Lehmann, G. and Nahrstedt, A. (1979). A new cyanogenic glycoside from *Hordeum vulgare. Phytochemistry* **18**: 1515-1517.
25. Fay, P.K. and Duke, W.B. (1977). An assessment of allelopathic potential in *Avena* germplasm. *Weed Science* **25**: 224-228.
26. Fischbeck, G. (2002). Contribution of barley to agriculture: a brief overview. In: *Barley Science* (Eds., G.A. Slafer, J.L. Molina-Cano, R. Savin, J.L. Araus and I. Romagosa), pp. 1-14. Food Products Press, Binghamton, NY.
27. Forslund, K. and Jonsson, L. (1997). Cyanogenic glycosides and their metabolic enzymes in barley, in relation to nitrogen levels. *Physologia Plantarum* **101**: 367-372.
28. Friedrich, W. and Galinsa, R. (2002). Identification of a new flavanol glucoside from barley (*Hordeum vulgare* L.) and malt. *European Food Research and Technology* **214**: 388-393.
29. Gibson, M.T., Welch, I.M., Barrett, P.R.F. and Ridge, I. (1990). Barley straw as an inhibitor of algal growth. II: Laboratory studies. *Journal of Applied Phycology* **2**: 241-248.

30. Gliessman, S.R. (2002). Allelopathy and agroecology. In: *Chemical Ecology of Plants: Alelopathy in Aquatic and Terrestial Ecosystems* (Eds., Inderjit and A.U. Mallik) pp. 173-185. Birkhäuser Verlag, Basel, Switzerland.
31. Glinwood, R., Gradin, T., Karpinska, B., Ahmed, E., Jonsson, L. and Ninkovic, V. (2007). Aphid acceptance of barley exposed to volatile phytochemicals differs between plants exposed in daylight and darkness. *Plant Signaling and Behavior* **2**: 321-326.
32. Greenland, A.J. and Lewis, D.H. (1984). Amines in barley leaves infected with brown rust and their possible relevance to formation of 'green islands'. *New Phytologist* **96**: 283-291.
33. Grün, S., Frey, M. and Gierl, A. (2005). Evolution of the indole alkaloid biosynthesis in the genus *Hordeum*: distribution of gramine and DIBOA and isolation of the benzoxazinoid biosynthesis genes from *Hordeum lechleri*. *Phytochemistry* **66**: 1264-1272.
34. Gubbels, G.H. and Kenaschuk, E.O. (1989). Agronomic performance of flax grown on canola, barley and flax stubble with and without tillage prior to seeding. *Canadian Journal of Plant Science* **69**: 31-38.
35. Hanson, A.D., Traynor, P.L., Ditz, K.M. and Reicosky, D.A. (1981). Gramine in barley forage – Effects of genotype and environment. *Crop Science* **21**: 726-730.
36. Hanson, A.D., Ditz, K.M., Singletary, G.W. and Leland, T.J. (1983). Gramine accumulation in leaves of barley grown under high-temperature stress. *Plant Physiology* **71**: 896-904.
37. Harborne, J.B. (1967). *Comparative Biochemistry of the Flavonoids*, Academic Press, London. 383 pp.
38. Harborne, J.B. and Williams, C.A. (2000). Advances in flavonoid research since 1992. *Phytochemistry* **55**: 481-504.
39. Hatcher, P.E. and Melander, B. (2003). Combining physical, cultural and biological methods: Prospects for integrated non-chemical weed management strategies. *Weed Research* **43**: 303-322.
40. Hoult, A.H.C. and Lovett, J.V. (1993). Biologically active secondary metabolites of barley. III. A method for identification and quantification of hordenine and gramine in barley by high-performance liquid chromatography. *Journal of Chemical Ecology* **19**: 2245-2254.
41. Hura, T., Dubert, F., Dabkowska, T., Stupnicka-Rodzynkiewicz, E., Stoklosa, A. and Lepiarczyk, A. (2006). Quantitative analysis of phenolics in selected crop species and biological activity of these compounds evaluated by sensitivity of *Echinochloa crus-galli*. *Acta Physiologiae Plantarum* **28**: 537-545.
42. Kimber, R.W.L. (1973). Phytotoxicity from plant residues. II. The effect of time of rotting straw from some grasses and legumes on the growth of wheat seedlings. *Plant and Soil* **38**: 347-361.
43. Kobsa, J. and Einhellig, F.A. (1987). The effects of ferulic acid on the mineral nutrition of grain sorghum. *Plant Physiology* **98**: 99-109.
44. Kremer, R.J. (2000). Growth suppression of annual weeds by deleterious rhizobacteria integrated with cover crops. In: *Proceedings of the X International Symposium on Biological Control of Weeds* (Ed., N.R. Spencer), pp. 931-940. Montana State University, Bozeman, MT.
45. Kremer, R.J. (2002). Bioherbicides – Potential successful strategies for weed control. In: *Microbial Biopesticides* (Eds., O. Koul and G. Dhaliwal), pp. 307-323. Taylor & Francis, London.
46. Légère, A. and Stevenson, F.C. (2002). Residual effects of crop rotation and weed management on a wheat test crop and weeds. *Weed Science* **50**: 101-111.
47. Liebman, M. and Robichaux, R.H. (1990). Competition by barley and pea against mustard: Effects on resource acquisition, photosynthesis and yield. *Agriculture, Ecosystems and Environment* **31**: 155-172.
48. Liebman, M. and Mohler, C.L. (2001). Weeds and the soil environment. In: *Ecological Management of Agricultural Weeds* (Ed., M. Liebman, C.L. Mohler and C.P. Staver), pp. 210-268. Cambridge University Press, Cambridge, UK.
49. Liu, D.L. and Lovett, J.V. (1993a). Biologically active secondary metabolites of barley. I. Developing techniques and assessing allelopathy in barley. *Journal of Chemical Ecology* **19**: 2217-2230.
50. Liu, D.L. and Lovett, J.V. (1993b). Biologically active secondary metabolites of barley. II. Phytotoxicity of barley allelochemicals. *Journal of Chemical Ecology* **19**: 2231-2244.
51. Liu, L., Gitz, D.C. III and McClure, J.W. (1995). Effects of UV-B on flavonoids, ferulic acid, growth and photosynthesis in barley primary leaves. *Physiologia Plantarum* **93**: 725-733.
52. Lovett, J.V. and Hoult, A.H.C. (1995). Allelopathy and self-defense in barley. In: *Allelopathy – Organisms, Processes and Applications* (Eds., Inderjit, K.M.M. Dakshini and F.A. Einhellig). ACS Symposium Series **582**: 170-183. American Chemical Society, Washington, DC.
53. Lovett, J.V., Hoult, A.H.C. and Christen, O. (1994). Biologically active secondary metabolites of barley. IV. Hordenine production by different barley lines. *Journal of Chemical Ecology* **20**: 1945-1954.

54. Lynch, J.M. (1978). Production and phytotoxicity of acetic acid in anaerobic soils containing plant residues. *Soil Biology and Biochemistry* **10**:131-135.
55. Macías, F.A., Molinillo, J.M.G., Varela, R.M. and Galindo, J.C.G. (2007). Allelopathy – a natural alternative for weed control. *Pest Management Science* **63**: 327-348.
56. Mann, H.H. and Barnes, T.W. (1952). The competition between barley and certain weeds under controlled conditions. V. Competition with clover considered as a weed. *Annals of Applied Biology* **39**: 111-119.
57. Mann, J.D., Steinhart, C.E. and Mudd, S.H. (1963). Alkaloids and plant metabolism. IV. The distribution and formation of tryamine methylpherase during germination of barley. *Journal of Biological Chemistry* **238**: 676-681.
58. Marinova, K., Kleinschmidt, K., Weissenböch, G. and Klein, M. (2007). Flavonoid biosynthesis in barley primary leaves requires the presence of the vacuole and controls the activity of vacuolar flavonoid transport. *Plant Physiology* **144**: 432-444.
59. Molina-Cato, J.L., Igartua, E., Casas, A-M. and Moralejo, M. (2002). New views on the origin of cultivated barley. In: *Barley Science* (Eds., G.A. Slafer, J.L. Molina-Cano, R. Savin, J.L. Araus and I. Romagosa), pp. 15-29. Food Products Press, Binghamton, NY.
60. Nielsen, K.A., Olsen, C.E., Pontoppidan, K. and Moller, B.L. (2002). Leucine-derived cyano glucosides in barley. *Plant Physiology* **129**: 1066-1075.
61. Ohashi, H., Yamamoto, E., Lewis, N.g., and Towers, G.H.N. (1987). 5-Hydroxyferulic acid in *Zea mays* and *Hordeum vulgare* cell walls. *Phytochemistry* **26**: 1915-1916.
62. Osawa, T., Katsuzaki, H., Hagiwara, Y., Hagiwara, H. and Shibamoto, T. (1992). A novel antioxidant isolated from young green barley leaves. *Journal of Agricultural and Food Chemistry* **40**: 1135-1138.
63. Oueslati, O., Ben-Hammouda, M., Ghorbal, M.H., El Gazzeh, M. and Kremer, R.J. (2005). Barley autotoxicity as influenced by varietal and seasonal variation. *Journal of Agronomy and Crop Science* 191: 249-254.
64. Oueslati, O., Ben-Hammouda, M., Ghorbal, M.H., El Gazzeh, M. and Kremer, R.J. (2009). Role of phenolic acids in expression of barley (*Hordeum vulgare*) autotoxicity. *Allelopathy Journal* **23**: 157-166.
65. Oveisi, M., H.R. Mashhadi, Baghestani, M.A., Alizadeh, H.M. and Badri, S. (2008). Assessment of the allelopathic potential of 17 Iranian barley cultivars in different development stages and their variations over 60 years of selection. *Weed Biology and Management* **8**: 225-232.
66. Overland, L. (1966). The role of allelopathic substances in the "smother crop" barley. *American Journal of Botany* **53**: 423-432.
67. Patrick, Z.A., Toussoun, T.A. and Snyder, W.C. (1963). Phytotoxic substances in arable soils associated with decomposition of plant residues. *Phytopathology* **63**: 152-161.
68. Patterson, D.T. (1989). Effects of allelopathic chemicals on growth and physiological responses of soybean (*Glycine max*). *Weed Science* **29**: 53-59.
69. Perez, F.J. and Ormeno-Nunez, J. (1993). Weed growth interference from temperate cereals: The effect of a hydroxamic acids-exuding rye (*Secale cereale* L.) cultivar. *Weed Research* **33**: 115-119.
70. Pettersson, J., Ninkovic, V. and Ahmed, E. (1999). Volatiles from different barley cultivars affect aphid acceptance of neighboring plants. *Acta Agriculturae Scandinavica Section B. Soil and Plant Sciences* **49**: 152-157.
71. Pfirter, H.A., Ammon, H.U., Guntli, D., Greaves, M.P. and Defago, G. (1997). Towards the management of field bindweed (*Convolvulus arvensis*) and hedge bindweed (*Calystegia sepium*) with fungal pathogens and cover crops. *Integrated Pest Management Review* **2**: 61-69.
72. Poehlman, J.M. and Helm, C.A. (1947). *Winter Barley in Missouri*. Missouri Agricultural Experiment Station Bulletin 508. 18 pp. University of Missouri, Columbia, MO.
73. Poehlman, J.M. (1985). Adaptation and distribution. In: *Barley* (Ed., D.C. Rasmussen) pp. 1-18. American Society of Agronomy, Madison, WI.
74. Pourmohseni, H., Ibenthal, W.D., Machinek, R., Remberg, G. and Wray, V. (1993). Cyanoglucosides in the epidermis of *Hordeum vulgare. Phytochemistry* **33**: 295-297.
75. Putnam, A.R. and Duke, W.B. (1978). Allelopathy in agroecosystems. *Annual Review of Phytopathology* **16**: 431-451.
76. Putnam, A.R. and DeFrank, J. (1983). Use of phytotoxic plant residues for selective weed control. *Crop Protection* **2**: 173-181.
77. Putnam, A.R., DeFrank, J. and Barnes, J.P. (1983). Exploitation of allelopathy for weed control in annual and perennial cropping systems. *Journal of Chemical Ecology* **9**: 1001-1010.

78. Read, J.J. and Jensen, E.H. (1989). Phytotoxicity of water-soluble substances from alfalfa and barley soil extracts on four crop species. *Journal of Chemical Ecology* **15**: 619-628.
79. Reid, D.A. 1985). Morphology and anatomy of the barley plant. In: *Barley* (Ed., D.C. Rasmussen), pp. 73-101. American Society of Agronomy, Madison, Wisconsin, USA.
80. Rice, E.L. (1984). *Allelopathy*. 2nd Ed. Academic Press, Orlando, FL. 422 pp.
81. Salas, M.L. and Corcuera, L.J. (1991). Effect of environment on gramine content in barley leaves and susceptibility to the aphid *Schizaphis graminum. Phytochemistry* **30**: 3237-3240.
82. Saunders, J.A. and McClure, J.W. (1976). The occurrence and photoregulation of flavonoids in barley plastids. *Phytochemistry* **15**: 805-807.
83. Sepulveda, B.A. and Corcuera, L.J. (1990). Effect of gramine on the susceptibility of barley leaves to *Pseudomonas syringae. Phytochemistry* **29**: 465-467.
84. Smith, T.A. and Best, G.R. (1978). Distribution of the hordatines in barley. *Phytochemistry* **17**: 1093-1098.
85. Stoessl, A. (1965). The antifungal factors in barley – III. Isolation of *p*-coumaroylagmatine. *Phytochemistry* **4**: 973-976.
86. Vancura, V. (1964). Root exudates of plants I. Analysis of root exudates of barley and wheat in their initial phases of growth. *Plant and Soil* **21**: 231-248.
87. Vasilakoglou, I. and Dhima, K. (2008). Forage yield and competition indices of berseem clover intercropped with barley. *Agronomy Journal* **100**: 1749-1756.
88. Velozo, J.A., Alvarez, R.I., Wächter, G.A., Timmermann, B.N. and Corcuera, L.J. (1999). Increase in gramine content in barley infested by the aphid *Schizaphis graminum* R. *Phytochemistry* **52**: 1059-1061.
89. Von Bothmer, R. and Jacobsen, N. (1985). Origin, taxonomy and related species. In: *Barley* (Ed., D.C. Rasmussen) pp. 19-56. American Society of Agronomy, Madison, WI.
90. Von Ropenack, E., Parr, A. and Schulze-Lefert, P. (1998). Structural analysis and dynamics of soluble cell wall bound barley phenolics and their role in broad spectrum resistance to the powdery mildew fungus. *Journal of Biological Chemistry* **273**: 9013-9022.
91. Walters, D.R. (2003). Polyamines and plant disease. *Phytochemistry* **64**: 97-107.
92. Walters, D.R. and Wylie, M.A. (1986). Polyamines in discrete regions of barley leaves infected with the powdery mildew fungus *Erysiphe graminis. Physiologia Plantarum* **67**: 630-633.
93. Weiel, J. and Hapner, K.D. (1976). Barley proteinase inhibitors: a possible role in grasshopper control? *Phytochemistry* **15**: 1885-1887.
94. Weih, M., Didon, U.M.E., Rönnberg-Wästljung, A.-C. and Björkman, C. (2008). Integrated agricultural research and crop breeding: allelopathic weed control in cereals and long-term productivity in perennial biomass crops. *Agricultural Systems* **97**: 99-107.
95. Welch, I.M., Barrett, P.R.F., Gibson, M.T. and Ridge, I. (1990). Barley straw as an inhibitor of algal growth I: studies in the Chesterfield Canal. *Journal of Applied Phycology* **2**: 231-239.
96. Weston, L.A. (2005). History and current trends in the use of allelopathy for weed management. *HortTechnology* **15**: 529-534.
97. Weston, L.A. and Duke, S.O. (2003). Weed and crop allelopathy. *Critical Reviews in Plant Sciences* **22**: 367-389.
98. Wippich, C. and Wink, M. (1985). Biological properties of alkaloids. Influence of quinolizidine alkaloids and gramine on the germination and development of powdery mildew, *Erysiphe graminis* f.sp. *hordei*. *Experientia* **41**: 1477-1479.
99. Wu, H., Pratley, J., Lemerle, D. and Haig, T. (1999). Crop cultivars with allelopathic activity. *Weed Research* **39**: 171-180.
100. Yoshida, H., Tsumuki, H., Kanehisa, K. and Corcuera, L.J. (1993). Release of gramine from the surface of barley leaves. *Phytochemistry* **34**: 1011-1013.
101. Yu, J., Vasanthan, T. and Temelli, F. (2001). Analysis of phenolic acids in barley by high-performance liquid chromatography. *Journal of Agricultural and Food Chemistry* **49**: 4352-4358.
102. Zúñiga, G.E., Varaanda, E.M. and Corcuera, L.J. (1988). Effect of gramine on the feeding behavior of the aphids *Schizaphis graminum* and *Rhopalosiphum padi. Entomologia Experimenatlis et Applicata* **47**: 161-165.