Molecular approaches in improving wheat allelopathy

Hanwen Wu[1]

[1]Leslie Research Centre, Department of Primary Industries and Fisheries, PO Box 2282, Toowoomba, QLD 4350, Australia. Email: hanwen.wu@dpi.qld.gov.au

Abstract

The rapid development of herbicide resistance in weed species has posed an increasing threat to sustainable agricultural production. Crop allelopathy provides a viable alternative in managing resistant weed populations. Crop plants can produce and exude allelochemicals into their surroundings to suppress weed growth. Wheat (*Triticum aestivum*), as one of the world's important crops, has been studied in depth for its allelopathic potential in weed management. Research on wheat allelopathy has progressed rapidly from the initial evaluation of allelopathic potential to the identification of allelochemicals and genetic markers associated with wheat allelopathy. Allelopathic activity varied among wheat accessions. Significant varietal differences in the production of allelochemicals were also found. In comparison with weakly allelopathic accessions, strongly allelopathic accessions produced significantly higher amounts of allelochemicals in the shoots or roots of young seedlings, and also exuded larger amounts of allelochemicals into the growth medium. Two major quantitative trait loci (QTLs) associated with wheat allelopathy have been identified. Recent advances in metabolomics, transcriptomics and proteomics will greatly assist in the identification of genes encoding the biosynthesis of allelochemicals. Plant cytochrome P450s catalyse myriad biosynthetic pathways of plant secondary metabolites. A number of cytochrome P450s have been reported and cDNAs of these P450s are now readily available for further identification of new P450 families and subfamilies. The cloned cDNA genes could be manipulated to regulate the biosynthesis of allelochemicals, thereby resulting in better weed suppression via elevated levels of allelopathic potential in commercial wheat cultivars.

Media summary

Wheat allelopathy has great potential in integrated weed management. Concerted research efforts have been made toward the development of wheat cultivars with high allelopathic activity.

Key Words

Triticum aestivum, allelopathy, weed management, allelochemicals, cytochrome P450, gene expression.

Introduction

The extensive use of herbicides in modern agriculture has given rise to concerns about herbicide residues in the environment and the rapid development of herbicide resistance. Globally, over 295 weed biotypes have now been reported to have acquired resistance to important herbicides. At least 177 weeds species, including 106 dicots and 71 monocots, have evolved resistance to herbicides (Heap 2005). Annual ryegrass (*Lolium rigidum*), the most widespread and troublesome weed of Australian agriculture, has developed resistance to 9 major herbicide groups, including glyphosate (Heap 2005). The emergence of herbicide resistant weed species is therefore threatening sustainable agricultural production and has resulted in increased economic loss and associated ecological problems. Non-herbicidal innovations, such as enhancing crop allelopathic ability, are increasingly needed in managing weed populations (Wu et al. 1999a and 2003a).

The role of allelopathy in weed management has gained a great deal of attention over the last two decades (Wu et al. 1999a; Bertholdsson 2005). Weed suppression by crop allelopathy during the early establishment period could reduce the need for commercial herbicides to early season application, with late season weed control provided by the heightened advantages of crop competitiveness. The genetic enhancement of crop allelopathy for weed management has been highlighted (Duke et al. 2001).

Wheat (*Triticum aestivum* L.), as one of the major food crops in the world, has been examined internationally for its allelopathic potential in weed suppression (Wu et al. 2000b; Belz and Hurle 2004; Bertholdsson 2004). Early studies in the late 1960s found that residue allelopathy varied among wheat cultivars (Guenzi et al. 1967; Kimber 1967). Wu et al. (2003a) found that aqueous extracts of shoot residues derived from certain wheat cultivars significantly inhibited the germination and root growth of a susceptible biotype of *L. rigidum*, as well as a biotype of this weed resistant to a number of chemically distinct herbicides. To date, research on wheat allelopathy has progressed rapidly from the initial phase of evaluation of wheat allelopathy (Wu et al. 2000b; Wu et al. 2003a), to the identification of wheat allelochemicals (Wu et al.2000c, 2001a, b and c) and degradation of these compounds (Fomsgaard et al. 2004), and further to the identification of genetic markers associated with wheat allelopathy (Wu et al. 2003b). This paper summarises recent advances in wheat allelopathy research and identifies the need for applying molecular technology in this fascinating research area.

Differential allelopathic activity in wheat germplasm

Wheat seedlings produce and release toxic root exudates inhibitory to a number of weed species (Spruell 1984; Wu et al. 2000b; Belz and Hurle 2004; Bertholdsson 2005). Spruell (1984) evaluated the allelopathic potential of wheat root exudates on the growth of *Bromus japonicus* and *Chenopodium album*. Differential allelopathic effects were found in 286 wheat accessions and one accession inhibited the growth of *B. japonicus* by up to 53% when compared to a non-allelopathic cultivar.

A novel screening bioassay, the ‘equal-compartment-agar-method’ (ECAM), was developed to assess wheat seedling allelopathy on *L. rigidum* (Wu et al. 2000a). ECAM successfully separates allelopathic effects from competitive effects between crop and weed plants, and enables the constant release and accumulation of allelochemicals from living wheat seedlings into the growth medium, thereby affecting the growth of *L. rigidum*. This simple bioassay was employed to evaluate seedling allelopathy against *L. rigidum* in a worldwide collection of 453 wheat accessions originating from fifty countries (Wu et al. 2000b). Results showed that wheat accessions differed significantly in their seedling allelopathy, with the inhibition of root growth of ryegrass ranging from 10% to 91%.

Bertholdsson (2004) employed a similar agar-based screening bioassay to determine the variation in allelopathic activity of root exudates among 1104 wheat accessions from Africa, South America, Asia, the former Soviet Union,

America, Sweden and other European countries. He found that certain wheat genotypes can produce toxic root exudates, inhibiting the root growth of perennial ryegrass (*Lolium perenne* L.) by as much as 50-60%. Similarly, Belz and Hurle (2004) designed a dose-response bioassay using hydroponic culture to assess the allelopathic activity of wheat root exudates and found that wheat accessions differed in their allelopathic activity on the root growth of *Sinapis alba* L. An increasing trend in potential allelopathic activity was found in spring wheat during 100 years of breeding, although there is a decreasing trend in barley (Bertholdsson 2005). The high allelopathic activity in some modern spring wheat cultivars could be incorporated into high yielding wheat lines for better weed suppression.

Differential wheat allelopathy has also been demonstrated in field trials. Using a pot screening bioassay, Rizvi et al. (2004) found that 200 wheat accessions varied in their allelopathic activity in the field. Some accessions inhibited weed growth by up to 75%, achieving similar results to hand weeding. These results demonstrated that wheat allelopathy can be used to reduce weed populations below the threshold level to minimise the applications of herbicides.

Differential production of allelochemicals in wheat germplasm

Advanced analytical instruments have greatly assisted the identification of a number of allelochemicals in wheat (Wu et al. 1999b). Significant genetic variations in the production of phenolic compounds and benzoxazinones (Bxs) were reported among 58 wheat accessions previously found with varied allelopathic potential (Wu et al. 2000c; 2001a and b). The difference in the concentration of allelochemicals depends largely on the chemicals and accessions analysed (Table 1). The concentration can be up to 68 times of difference in shoots, 41 times in roots, and 70 times in root exudates.

Benzoxazinones, a novel class of alkaloids, were identified as biologically active agents conferring weed suppression (Perez 1990). 2,4-Dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and its decomposition product 6-methoxybenzoxazolin-2-one (MBOA) inhibited root growth of wild oats (*Avena fatua*). Huang et al. (2003) reported that two Bxs DIMBOA and 2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA) were more inhibitory to *L. rigidum* than the natural lactam benzoxazinones, 2-hydroxy-1,4-benzoxazin-3-one (HBOA) and 2-hydroxy-7-methoxy-1,4-benzoxazin-3-one (HMBOA). The lower phytotoxicity of HBOA and HMBOA is believed to be associated with the absence of an important OH group on position 4 of the oxazinone ring.

Wheat varietal difference in the production of Bxs has been well documented (Nicol et al. 1992; Wu et al. 2001b). DIMBOA content in the shoots or the roots differed significantly between wheat accessions (Wu et al. 2001b). The variation of the DIMBOA concentration was similar in shoots and roots of young wheat seedlings, ranging from no detectable amount to 730 mg/kg dry matter. Forty-seven out of the 58 accessions did not exude detectable amounts of DIMBOA through their living roots into a growth medium, although substantial levels of DIMBOA were found in the respective shoot or root tissues. Only 11 accessions were capable of exuding varied amounts of DIMBOA into the growth medium. These results demonstrated that the exudation of DIMBOA by living wheat roots was highly accession-dependent, indicating that genetic factors govern the exudation process of DIMBOA.

Table 1. Variation in allelochemical concentration in 58 wheat accessions.

	Shoot (mg/kg of dry matter)			Root (mg/kg of dry matter)			Root exudates (mg/L of water agar)		
Allelochemicals	Range	Average	Ratio[a]	Range	Average	Ratio	Range	Average	Ratio
PHB	9.8 - 49.3	31.1	5.0	24.5 - 94.5	52.5	3.9	2.3 - 18.6	7.1	8.0

VAN	12.9 - 68.8	42.0	5.3	19.9 - 91.7	61.0	4.6	0.6 - 17.5	7.3	28.7
cis-COU	0.8 - 11.2	4.2	13.5	3.7 - 15.4	7.1	4.1	0.1 - 4.9	1.1	69.9
SYR	1.9 - 61.5	22.9	32.6	2.2 - 38.6	10.4	17.8	nd - 52.7	21.1	N/A
cis-FER	0.3 -17.0	5.2	68.0	1.0 - 42.2	8.7	40.6	0.3 - 12.7	2.8	38.5
trans-COU	11.4 - 117.7	38.5	10.3	19.3 - 183.6	69.4	9.5	1.5 - 20.5	6.2	13.6
trans-FER	3.2 - 149.3	74.1	46.5	11.7 - 187.6	97.7	16.0	1.6 - 23.4	9.9	14.6
DIMBOA	nd - 730.4	439.4	n/a	nd - 734.1	643.0	n/a	nd-	30**	N/A

Note: [a]Ratio--highest/lowest concentration. Abbreviations are PHB for para-hydroxybenzoic acid, VAN for vanillic acid, COU for para-coumaric acid; SYR for syringic acid; FER for ferulic acid and DIMBOA for 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one.

Research has shown that wheat seedlings exuded varying amounts of phenolic acids into a growth medium (Wu et al. 2001c). In comparison with weakly allelopathic accessions, strongly allelopathic accessions produced significantly higher amounts of allelochemicals in the shoots or roots of the wheat seedlings, and also exuded larger amounts of allelochemicals into the growth medium (Wu et al. 2001a and c; 2002). Similarly, the amounts of Bxs exuded by different wheat cultivars showed a positive correlation with their allelopathic activity on the root growth of *S. alba* (Belz and Hurle 2004). The dynamic exudation of five Bxs and seven phenolic acids was monitored in root exudates of young wheat seedlings (Huang et al. 2003). The highest combined concentration of measured allelochemicals from both chemical groups occurred at day 8 after emergence, which coincides very well with the observed maximum growth inhibition of *L. rigidum* by wheat root exudates during this period. These results suggest a strong chemical basis involved in the allelopathic inhibition by root exudates.

Genetic control of wheat allelopathy

Genetic variations in wheat allelopathic activity and in the biosynthesis of allelochemicals have laid a solid foundation towards developing wheat cultivars with strong allelopathic potential. Although this ultimate breeding goal has not yet been achieved, progress has been made in understanding the genetic control of crop allelopathy. Wu et al. (2000b) studied the genetic control of wheat allelopathy using near isogenic wheat lines (NILs) derived from Hartog (weakly allelopathic) × Janz (strongly allelopathic). The allelopathic activity of BC_2-Hartog lines (backcrossed to Hartog) was weak, similar to that of Hartog. Similarly, Janz lines had strong allelopathic activity derived from Janz. These results suggest a strong chemical basis involved in the inhibition provoked by root exudates.

Complex biochemical pathways and distinct categories of allelopathic compounds indicate multiple genes are probably involved in the production of allelochemicals (Wu et al. 2000b). Genetic mapping of quantitative trait loci (QTLs) has shed light on the inheritance of allelopathy traits. QTLs conferring the allelopathic activity have been identified in wheat (Wu et al. 2003b) and rice (Jensen et al. 2001; Ebana et al. 2001). A doubled haploid (DH) population derived from cv. Sunco (weakly allelopathic) and cv. Tasman (strongly allelopathic) was developed to investigate the genetic control of wheat allelopathy (Wu et al. 2003b). Analysis of restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), and microsatellite (SSRs) markers identified two major QTLs on chromosome 2B associated with wheat allelopathy. Regression based on simple interval mapping revealed that one of the QLTs on chromosome 2B accounted for 29% of the total phenotypic variance of wheat seedling allelopathy (Wu et al. 2003b). In rice, Jensen et al. (2001) identified four QTLs on three rice chromosomes, explaining 35% of the total phenotypic variation of the allelopathic activity. Ebana et al. (2001) also identified seven

QTLs associated with rice allelopathic activity. A multiple model estimated that five QTLs explained 36.6% of the total phenotypic variation. These QTLs, once validated, can be used to improve genetic gains for the allelopathic activity through marker-assisted selection in crop breeding programmes.

Cytochrome P450 encoding biosynthesis of wheat secondary metabolites

Cytochrome P450s are a large group of heme-containing enzymes present in all kingdoms (Nelson 1999). They catalyse diverse biochemical reactions including hydroxylations, dehalogenations, dealkylations, deaminations and epoxidations, and are therefore involved in myriad biosynthetic pathways of plant secondary metabolites, such as the biosynthesis of pigments, antioxidants and defense compounds, which include phenylpropanoids, flavonoids, phenolic esters, coumarins, glucosinolates, cyanogenic glucosides, benzoxazinones, isoprenoids, alkaloids, terpenoids, lipids, and plant growth regulators such as gibberellins, jasmonic acid, and brassinosteroids (Chapple 1998; Kahn and Durst 2000). Examples of P450s involving the biosynthesis of plant secondary metabolites are given in Table 2. Many of these secondary metabolites are excellent lead molecules for herbicide development (Putnam 1988).

The growing interest in plant cytochrome has led to the identification of many plant P450s encoding the biosynthesis of defense compounds, including the notable Bxs in maize and wheat. The biosynthetic pathway of Bxs branches off from that of tryptophan at indole-3-glycerol phosphate. Five genes involved in the downstream reactions from indole-3-glycerol phosphate were isolated from maize and designated as *Bx*1– *Bx*5 (Frey et al. 1997). Bx1 encodes indole synthase homologous to the tryptophan synthase alpha subunit (TSA), whereas *Bx*2–*Bx*5 genes encode four cytochrome P450 monooxygenases (CYP71C1-CYP71C4) (Frey et al. 1997). Expression of cDNAs in yeast demonstrated that each of these cloned P450s catalysed sequential hydroxylation of indole to DIBOA.

Further study has demonstrated that two genes *Bx6* and *Bx7* are involved in the conversion of DIBOA to DIMBOA (Frey et al. 2003). *Bx6* encodes a 2-oxoglutarate-dependent dioxygenase that catalyses the hydroxylation of DIBOA at position 7. The resulting product (TRIBOA) is then methylated by the O-methyltransferase *Bx*7 to generate DIMBOA. Two glucosyltransferase genes *Bx8* and *Bx*9 are both able to catalyse the conversion of DIBOA and DIMBOA to DIBOAGlc and DIMBOAGlc, respectively (Rad et al. 2001). *Bx*s genes (*Bx*1-8), governing the entire DIMBOA biosynthesis, have been shown to cluster on the short arm of chromosome 4, although Bx 9 was located on chromosome 1 (Frey et al. 2003; Rad et al. 2001). A schematic biosynthetic pathway of DIMBOA is illustrated in Figure 1.

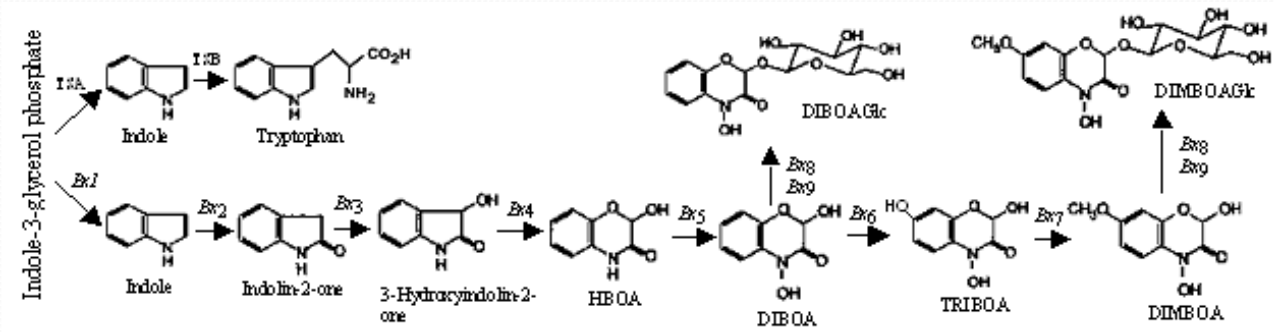

Figure 1. DIMBOA biosynthetic pathway in maize. TSA and TSB stand for the alpha and beta subunits of tryptophan synthase, respectively. *Bx*1 represents a tryptophan synthase activity, *Bx*2 to *Bx*5 represent cytochrome P450 monooxygenases; *Bx*6 and *Bx*7 encode 2-oxoglutarate-dependant dioxygenases, and *Bx*8 and *Bx*9 encode glucosyltransferases.

cDNAs of five P450s (CYP71C6, CYP71C7v2, CYP71C8v2, CYP71C9v1 and CYP71C9v2) involved in DIBOA biosynthesis were also isolated in wheat (Nomura et al. 2002). CYP71C9v1 and CYP71C9v2 shared 97% similarity in amino acid and nucleotide sequences. The cloned P450 species showed 76–79% identity at the amino acid level to the corresponding maize P450 species CYP71C1–C4, suggesting the common origin of DIBOA biosynthesis in wheat and maize. Nomura et al. (2003) further found that these cDNAs (TaBx1–TaBx5) genes were separately located on two groups of chromosomes in wheat. TaBx1 and TaBx2 co-existed in specific regions of chromosomes 4AS, 4BL and 4DL. TaBx3 genes were located on 5AS, 5BS, 5DS and 5BL, while TaBx4 and TaBx5 genes were located on the short arms of group-5 chromosomes.

Table 2. Plant cytochrome P450s encoding the biosynthesis of secondary metabolites. (http://members.shaw.ca/P450sinPlants**)**

P450	Pathway	Plant Species
CYP71C1-4	cyclic hydroxamic acid	corn
CYP71C6, C7v2, C8v2, C9v1 C9v2	cyclic hydroxamic acid	wheat
CYP71D12	indole alkaloid	periwinkle
CYP71D9	flavonoid/isoflavonoid	soybean
CYP71E1	cyanogenic glucoside	sorghum
CYP72A1	indole alkaloid	periwinkle
CYP73A5	phenylpropanoid	*Arabidopsis thaliana*
CYP75A1	phenylpropanoid	petunia
CYP75B1	phenylpropanoid	*Arabidopsis thaliana*
CYP76B6	terpenoid indole alkaloid	periwinkle
CYP79A1	cyanogenic glucoside	sorghum
CYP79A2	benzylglucosinolate	*Arabidopsis thaliana*
CYP79B2	indole glucosinolate	*Arabidopsis thaliana*
CYP79D1 / D2	cyanogenic glucosides	cassava
CYP79E1 / E2	cyanogenic glucosides	seaside arrow grass
CYP79F1	aliphatic glucosinolate	*Arabidopsis thaliana*
CYP80B1	alkaloid	California poppy
CYP81E1	flavonoid/isoflavonoid	licorice
CYP83A1	indole glucosinolate	*Arabidopsis thaliana*
CYP84A1	phenylpropanoid	*Arabidopsis thaliana*
CYP85	brassinosteroid biosynthesis	tomato

CYP85A1	brassinolide	*Arabidopsis thaliana*
CYP86A1	fatty acids	*Arabidopsis thaliana*
CYP90A1	brassinolide	*Arabidopsis thaliana*
CYP90B1	brassinolide	*Arabidopsis thaliana*
CYP90D2	brassinosteroid biosynthesis	rice
CYP92A6	brassinosteroid biosynthesis	pea
CYP93A1	pterocarpanoid phytoalexin biosythesis	soybean
CYP93B1	flavonoid/isoflavonoid	licorice
CYP93C1	isoflanoids	soybean
CYP94A5	fatty acids	tobacco
CYP96C1	terpenoid indole alkaloid	periwinkle
CYP97C1	carotenoid	*Arabidopsis thaliana*
CYP98A3	phenypropanoid	*Arabidopsis thaliana*
CYP706B1	sesquiterpene biosynthesis	cotton

Since the cloning of the first plant P450 gene in 1990, there has been an explosion in the rate at which genes encoding plant P450s have been identified. Many P450 genes have been identified using PCR (Baltrusch et al. 1997; Hutvágner et al. 1997) and low-stringency hybridization with previously identified P450 probes (Udvardi et al. 1994; Czernic et al. 1996). In some cases, P450 genes have been identified by differential screening or differential display (Vetter et al. 1992; Suzuki et al. 1996). Other P450s have been identified among expressed sequence tag (EST) libraries (Shen et al. 1994; Cooke et al. 1996). Application of these molecular techniques will rapidly assist in identifying new P450 families and subfamilies encoding biosynthesis of plant secondary metabolites such as allelochemicals.

Overexpression of these P450 genes may modify the flux through biosynthetic pathways that give rise to accumulation of allelochemicals. Alternatively, the introduction of foreign P450 genes into alternative host plants may allow for the engineering of novel biochemical pathways and the synthesis of potent allelochemicals for weed suppression.

Discussion

Molecular and biochemical approaches are now being rapidly applied to allelopathy research. DNA microarray technology has been used extensively in gene expression profiling, and in the identification and genotyping of polymorphisms (Aharoni and Vorst 2001). This technology allows the simultaneous detection of the expression of thousands of genes. On the other hand, metabolomics, the unbiased identification and quantitation of all the metabolites, has emerged as a viable counterpart to proteomics and transcriptomics (Weckwerth 2003; Goodacre et al. 2004). Gene expression profiling techniques, coupling with the metabolite analysis, have been used to map novel structural and regulatory genes in the biochemical pathways of specific plant metabolites, such as alkaloids, flavonoids, and isoprenoids (Ohlrogge and Benning 2000; Forkmann and Martens 2001). Linking changes in

metabolite profiles to parallel analysis of gene expression through DNA microarray analysis provides possibilities for assigning gene functions based on cellular dynamics (Dixon 2001).

Crops have not yet been engineered to enhance the biosynthesis of allelochemicals for weed control, although they have been made resistant to insects, pathogens, and herbicides with transgenes. For example a gene from *Bacillus thuringiensis* (Bt) has been successfully engineered into cotton to produce insecticidal toxin (Perlak et al. 2001). The successful metabolic engineering of monoterpene biosynthesis to enhance scent and flavour in flowers and fruits has demonstrated the possibilities to engineer metabolic pathways to enhance the production of natural compounds for weed control (Canel 1999; Mahmoud and Croteau 2002).

Although crop cultivars with elevated level of allelopathy via increased biosynthesis of allelochemicals are not expected to provide complete control on weeds, the introduction of such cultivars should have a long-term impact on weed management (Wu et al. 2003a). The constant exposure of weed plants to the continuously released allelochemicals even at low concentrations would create a chemically-stressed condition for the weed, thereby altering the normal weed life cycle and resulting in poor growth vigour, reduction in weed seed production and replenishment into soil seedbank. Small changes in seed production will significantly influence the size of seedbank and reduce subsequent weed pressure (Gonzalez-Andujar and Fernandez-Quintanilla 2004).

References

Aharoni A and Vorst O (2001). DNA microarrays for functional plant genomics. *Plant Molecular Biology* **48,** 99-118.

Baltrusch M, Fulda M,Wolter FP and Heinz E (1997). Cloning and sequencing of a cytochrome P450 from *Pisum sativum* L. (Accession No. Z49263). *Plant Physiology* **114,** 1568.

Belz R and Hurle K (2004). Is there a benzoxazinone-mediated potential for weed-suppression in *Triticum* L. spp. and *secale cereale* L.? In 'Proceedings of Second European Allelopathy Symposium – Allelopathy: from understanding to application'. p98. Pulawy, Poland, June 4, 2004.

Bertholdsson NO (2004). Variation in allelopathic activity in spring wheat. In 'Proceedings of Second European Allelopathy Symposium – Allelopathy: from understanding to application'. p22. Pulawy, Poland, June 4, 2004.

Bertholdsson NO (2005). Early vigour and allelopathy - two useful traits for enhanced barley and wheat competitiveness with weeds. *Weed Research* **45,** 94-102.

Canel C (1999). From genes to phytochemicals: the genomics approach to the characterization and utilization of plant secondary metabolism. ISHS *Acta Horticulturae* **500,** 51-58.

Chapple C (1998). Molecular-genetic analysis of plant cytochrome p450-dependent monooxygenases. *Annual Review of Plant Physiology and Plant Molecular Biology* **49,** 311-343.

Cooke R, Raynal M, Laudie M, Grellet F, Delseny, M et al. (1996). Further progress towards a catalogue of all *Arabidopsis* genes: analysis of a set of 5000 nonredundant ESTs. *Plant Journal* **9,** 101-124.

Czernic P, Moliere F and Marco Y (1996). Structural organization of a genomic clone encoding a cytochrome P450-dependent monooxygenase from *Nicotiana tabacum* (Accession No. X96784) (PGR96–034). *Plant Physiology* **111,** 652.

Dixon RA (2001). Natural products and plant disease resistance. *Nature* **411,** 843-847.

Duke SO, Scheffler BE, Dayan FE and Ota E (2001.) Strategies for using transgenes to produce allelopathic crops.

Weed Technology **15,** 826–834.

Ebana K, Yan WG, Dilday RH, Namai H and Okuno K (2001). Analysis of QTL associated with the allelopathic effect of rice using water-soluble extracts. *Breeding Science* **51,** 47-51.

Fomsgaard IS, Mortensen AG and Carlsen SCK (2004). Microbial transformation products of benzoxazolinone and benzoxazinone allelochemicals - a review. *Chemosphere* **54,** 1025-1038.

Forkmann G and Martens S (2001). Metabolic engineering and applications of flavonoids. *Current Opinion in Biotechnology* **12,** 155-160.

Frey M, Chomet P, Glawischnig E, Stettner C, Grün S, Winklmair A, Eisenreich W, Bacher A, Meeley RB, Briggs SP, Simcox K and Gierl A (1997). Analysis of a chemical plant defense mechanism in grasses. *Science* **277,** 696-699

Frey M, Huber K, Park WJ, Sicker D, Lindberg P, Meeley RB, Simmons CR, Yalpani N and Gierl A (2003). A 2-oxoglutarate-dependent dioxygenase is integrated in DIMBOA-biosynthesis. *Phytochemistry* **62,** 371-376.

Goodacre R, Vaidyanathan S, Dunn WB, Harrigan GG and Kell DB (2004). Metabolomics by numbers: acquiring and understanding global metabolite data. *Trends in Biotechnology* **22,** 245-252.

Gonzalez-Andujar JL and Fernandez-Quintanilla C (2004) Modelling the population dynamics of annual ryegrass (*Lolium rigidum*) under various weed management systems. *Crop Protection* **23,** 723–729.

Guenzi WD, McCalla TM and Norstadt FA (1967). Presence and persistence of phytotoxic substances in wheat, oat, corn and sorghum residues. *Agronomy Journal* **59,** 163-165.

Heap I (2005). The International Survey of Herbicide Resistant Weeds. Online. Internet. March 02, 2005. Available www.weedscience.com.

Huang Z, Haig T, Wu H, An M and Pratley J (2003). Correlation between phytotoxicity on annual ryegrass (*Lolium rigidum*) and production dynamics of allelochemicals within root exudates of an allelopathic wheat. *Journal of Chemical Ecology* **29,** 2263-2279.

Hutvágner G, Barta E and Bánfalvi Z (1997). Isolation and sequence analysis of a cDNA and a related gene for cytochrome P450 proteins from *Solanum chacoense*. *Gene* **188,** 247-252.

Jensen BL, Courtois B, Shen LS, Li ZK, Olofsdotter M and Mauleon RP (2001). Locating genes controlling allelopathic effects against barnyardgrass in upland rice. *Agronomy Journal* **93,** 21-26.

Kahn R and Durst F (2000). Function and evolution of plant cytochrome P450. *Recent Advances in Phytochemistry* **34,** 151-189.

Kimber RWL (1967). Phytotoxicity from plant residues. I. The influence of rotted wheat straw on seedling growth. *Australian Journal of Agricultural Research* **18**, 361-374.

Mahmoud SS and Croteau RB (2002). Strategies for transgenic manipulation of monoterpene biosynthesis in plants. *Trends in Plant Science* **7,** 366-373.

Nelson DR (1999). Cytochrome P450 and the individuality of species. *Archives of Biochemistry and Biophysics* **369,** 1-10.

Nicol D, Copaja SV, Wratten SD and Niemeyer HM (1992). A screen of worldwide wheat cultivars for hydroxamic acid levels and aphid antixenosis. *Annals of Applied Biology* **121,** 11-18.

Nomura T, Ishihara A, Imaishi H, Endo TR, Ohkawa H and Iwamura H (2002). Molecular characterization and chromosomal localization of cytochrome P450 genes involved in the biosynthesis of cyclic hydroxamic acids in hexaploid wheat. *Molecular Genetics and Genomics* **267,** 210-217.

Nomura T, Ishihara A, Imaishi H, Ohkawa H, Endo TR and Iwamura H (2003). Rearrangement of the genes for the biosynthesis of benzoxazinones in the evolution of *Triticeae* species, *Planta* **217,** 776-782

Ohlrogge J and Benning C (2000). Unraveling plant metabolism by EST analysis. *Current Opinion in Plant Biology* **3,** 224-228.

Perez FJ (1990). Allelopathic effect of hydroxamic acids from cereals on *Avena sativa* and *A. fatua*. *Phytochemistry* **29,** 773-776.

Perlak FJ, Oppenhuizen M, Gustafson K, Voth R, Sivasupramaniam S, Heering D, Carey B, Ihrig RA and Roberts JK (2001). Development and commercial use of Bollgard® cotton in the USA - early promises versus today's reality. *Plant Journal* **27,** 489-501.

Putnam AR (1988). Allelochemicals from plants as herbicides. *Weed Technology* **2,** 510-518.

Shen B, Carneiro N, Torres-Jerez I, Stevenson B, McCreery T, Helentjaris T, Baysdorfer C, Almira E, Ferl RJ, Habben JE and Larkins B (1994). Partial sequencing and mapping of clones from two maize cDNA libraries. *Plant Molecular Biology* **26,** 1085-1101.

Spruell JA (1984). Allelopathic potential of wheat accessions. *Dissertation Abstracts International, B Sciences and Engineering* **45,** 1102B.

Suzuki G, Ohta H, Kato T, Igarashi T, Sakai F, Shibata D, Takano A, Masuda T, Shioi Y and Takamiya K (1996). Induction of a novel cytochrome P450 (CYP93 family) by methyl jasmonate in soybean suspension-cultured cells. *FEBS Letter* **383,** 83-86.

Rad U von, Hüttl R, Lottspeich F, Gierl A and Frey M (2001). Two glucosyltransferases are involved in detoxification of benzoxazinoids in maize. *Plant Journal* **28,** 633-642.

Rizvi SJH, Ketata H, Bazazi D, Roostaii M and Pala M (2004). Weed suppressing ability of bread wheat genotypes under greenhouse and field conditions. In ‘Proceedings of Second European Allelopathy Symposium – Allelopathy: from understanding to application’. p25. Pulawy, Poland, June 4, 2004.

Udvardi MK, Metzger JD, Krishnapillai V, Peacock WJ and Dennis ES (1994). Cloning and sequencing of a full-length cDNA from *Thlaspi arvense* L. that encodes a cytochrome P450. *Plant Physiology* **105,** 755-756.

Vetter HP, Mangold U, Schroder G, Marner FJ, Werck-Reichhart D and Schroder J (1992). Molecular analysis and heterologous expression of an inducible cytochrome P450 protein from periwinkle (*Catharanthus roseus* L.). *Plant Physiology* **100,** 998-1007.

Weckwerth W (2003). Metabolomics in systems biology. *Annual Review of Plant Biology* **54,** 669-689.

Wu H, Pratley J, Lemerle D and Haig T (1999a). Crop cultivars with allelopathic capability. *Weed Research* **39,** 171-180.

Wu H, Pratley J, Haig T and An M (1999b). Simultaneous determination of phenolic acids and 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one by GC/MS/MS in wheat (*Triticum aestivum* L.). *Journal of chromatography A* **863,** 315-321.

Wu H, Pratley J, Lemerle D and Haig T (2000a). Laboratory screening for allelopathic potential of wheat (*Triticum aestivum*) accessions against annual ryegrass (*Lolium rigidum*). *Australian Journal of Agricultural Research* **51,** 259-266.

Wu H, Pratley J, Lemerle D and Haig T (2000b). Evaluation of seedling allelopathy in 453 wheat (Triticum aestivum)accessions against annual ryegrass (*Lolium rigidum*) by the equal-compartment-agar method. *Australian Journal of Agricultural Research* **51,** 937-944.

Wu H, Pratley J, Haig T, Lemerle D and An M (2000c). Allelochemicals in wheat (*Triticum aestivum* L.): Variation of phenolic acids in root tissues. *Journal of Agricultural & Food Chemistry* **48,** 5321-5325.

Wu H, Pratley J, Haig T, Lemerle D and An M (2001a). Allelochemicals in wheat (*Triticum aestivum* L.): Variation of phenolic acids in shoot tissues. *Journal of Chemical Ecology* **27,** 125-135.

Wu H, Pratley J, Haig T, Lemerle D and An M (2001b). Allelochemicals in wheat (*Triticum aestivum* L.): Production and exudation of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one. *Journal of Chemical Ecology* **27,** 1691-1700.

Wu H, Pratley J, Haig T, Lemerle D and An M (2001c). Allelochemicals in wheat (*Triticum aestivum* L.): Cultivar difference in the exudation of phenolic acids. *Journal of Agricultural & Food Chemistry* **49,** 3742-3745.

Wu H, Pratley J, Haig T, Lemerle D and An M (2002). Chemical basis for wheat seedling allelopathy on the suppression of annual ryegrass (*Lolium rigidum*). *Journal of Agriculture and Food Chemistry* **50,** 4567-4571.

Wu H, Pratley J and Haig T (2003a). Phytotoxic effects of wheat extracts on a herbicide-resistant biotype of annual ryegrass (*Lolium rigidum*). *Journal of Agriculture and Food Chemistry* **51,** 4610-4616.

Wu H, Pratley J, Ma W and Haig T (2003b) Quantitative trait loci and molecular markers associated with wheat allelopathy. *Theoretical and Applied Genetics* **107,** 1477-1481.

Previous Top Next

...

Search Site

Search...

Disclaimer | Privacy Statement | Terms & Conditions

The Regional Institute | Help/Feedback | Contact us | Sitemap Powered by Cirql