Udo Blum

Plant-Plant Allelopathic Interactions

Phenolic Acids, Cover Crops and Weed Emergence



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Udo Blum Department of Plant Biology North Carolina State University Raleigh, NC 27695-7612 USA udo_blum@ncsu.edu

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This book is dedicated to all who have labored and will labor in the field of plant–plant allelopathic interactions.

Preface

For part of my PhD thesis I characterized the distribution of tannic acids in soils underneath sumac (Rhus copallina L.) located in abandoned fields of central Oklahoma (Blum and Rice 1969). Large quantities of tannic acids were found in the litter and organic residues underneath sumac. Tannic acids, which are very water soluble, were also found in the soil to a depth of 75 cm, with a definite zone of concentration at 45–55 cm. The techniques utilized at the time to recover and guantify tannic acids were rudimentary, at best. Amounts below 400 ppm added to soils could not be recovered, even though concentrations as low as 33 ppm added to soils inhibited nodulation of red kidney beans (*Phaseolus vulgaris* L. "Burpee"). These observations and their implications to plant-plant allelopathic interactions intrigued me at the time and I made a promise to myself that I would take another look at this subject in the future. Around 1980 I was ready to fulfill that promise. For the next 20 plus years research in my laboratory was primarily focused on various aspects of plant-plant allelopathic interactions with an emphasis on seedling behavior, soil chemistry, and microbiology. This book is a summary and retrospective analysis of this research program.

Although research publications on allelopathy have increased at a phenomenal rate since the 1980s, what is generally lacking are in-depth analyses and integration of this literature. For example, a quick search of Science Citation Index yielded 112 publications between 1981 and 1990, 627 publications between 1991 and 2000, and 1,615 publications between 2001 and 2010. The terms "allelopathic interactions" yielded 6, 58, and 212 publications over the same time intervals. However, less than 10% of these 276 citations listed for allelopathic interactions could be classified as review papers for allelopathic interactions of higher plants. These reviews, with minor exceptions, summarized, described, pooled, and/or integrated data for plant-plant allelopathic interactions determined for different species, environments, and ecosystems utilizing a range of different methods/protocols. Such reviews are useful in that they can identify potential/likely mechanisms that may bring about plant-plant allelopathic interactions and provide general guidelines and directions for future research. However, to identify and determine actual mechanisms that control and/or regulate the expression of plant-plant allelopathic interactions within a given ecosystem requires in-depth quantitative analyses of individual ecosystem processes and their interactions utilizing consistent experimental protocols. The research described in this book is an attempt to do just that for one type of ecosystem.

This book does not provide a comprehensive review of the plant–plant allelopathic interaction literature. For a general review of this literature the reader may wish to read several of the following: Rice (1974, 1979, 1983, 1984, 1995), Putnam and Tang (1986), Waller (1987), Siqueria et al. (1991), Inderjit et al. (1995, 1999), Inderjit and Keating (1999), Macías et al. (1999, 2004), Reigosa et al. (2006), Fujii and Hiradate (2007), Willis (2007), and Zeng et al. (2008).

There are several things that are unique about this book:

- a. The general format is that of research papers published in scientific journals. The materials are organized in sections such as, Abstract, Introduction, Materials and Methods, and Results and Discussion.
- b. There are four chapters, including an introduction to allelopathic plant–plant interactions (Chapter 1). They all emphasize basic aspects of science, but Chapter 2 is more theoretical/hypothetical in nature, Chapter 3 is more practical in nature, and Chapter 4 integrates the information presented in Chapters 2 and 3 and suggests future direction for research in plant–plant allelopathic interactions.
- c. Comments regarding logic, reasons, and justifications, for various procedures used are provided throughout the book.
- d. The Scientific Method and its approach to research are emphasized. For example, instead of definitive conclusions at the end of the book cons and pros are provided so that readers can draw their own conclusions. The reader will also find an extended listing of if-then hypotheses, and
- e. Although a broad range of literature is included, the primary focus of this book is a summary and retrospective analysis of some 20 plus years of research on plant–plant allelopathic interactions at North Carolina State University.

The above format was chosen so that researchers, students, farmers, as well as layman interested in science, reduced tillage production, and plant–plant allelopathic interactions, in particular, can learn to appreciate and understand the nature of science, its benefits and limitations, and our present knowledge of the action of natural products such as phenolic acids in soil on plant growth and development.

Raleigh, NC August 19, 2010 Udo Blum

References

- Blum U, Rice EL (1969) Inhibition of symbiotic nitrogen-fixation by gallic and tannic acid and possible roles in old-field succession. Torrey Bot Club 96:531–544
- Fujii Y, Hiradate S (2007) Allelopathy: new concepts and methodology. Science Publishers, Enfield, NY

Inderjit, Keating KI (1999) Allelopathy: principles, procedures, processes, and promises for biological control. Adv Agro 67:141–231

Preface

- Inderjit, Daskshini KMM, Einhellig FA (1995) Allelopathy: organisms, processes, and applications. ACS symposium series, vol 582. American Chemical Society, Washington, DC
- Inderjit, Daskshini KMM, Foy CL (1999) Principles and practices in plant ecology: allelochemical interactions. CRC Press, Boca Raton, FL
- Macías FA, Galindo JGC, Molinillo JMG, Cutler H (1999) Recent advances in allelopathy I. A science for the future. Cádiz University Press, Puerto Real Cádiz, Spain
- Macías FA, Galindo JGC, Molinillo JMG, Cutler H (2004) Allelopathy: chemistry & modes of action of allelochemicals. CRC Press, Boca Raton, FL
- Putnam AR, Tang CS (1986) Science of allelopathy. Wiley, New York, NY
- Reigosa MJ, Pedrol N, Gonzalez L (2006) Allelopathy. A physiological process with ecological implications. Springer, Dordrecht, The Netherlands
- Rice EL (1974) Allelopathy. Academic Press, Orlando, FL
- Rice EL (1979) Allelopathy an update. Bot Rev 45:15-109
- Rice EL (1983) Pest control with nature's chemicals: allelochemics and pheromones in gardening and agriculture. University of Oklahoma Press, Norman, NY
- Rice EL (1984) Allelopathy. Academic Press, Orlando, FL
- Rice EL (1995) Biological control of weeds and plant diseases: advances in applied allelopathy. University of Oklahoma Press, Norman, NY
- Siqueira JO, Nair MG, Hammerschmidt R, Safir GR (1991) Significance of phenolic compounds in plant-soil-microbial systems. Crit Rev Plant Sci 10:63–121
- Waller GR (1987) Allelochemicals: role in agriculture and forestry. ACS symposium series, vol 330. American Chemical Society, Washington, DC
- Willis RJ (2007) The history of allelopathy. Springer, Dordrecht, The Netherlands
- Zeng RS, Mallik AU, Luo SM (2008) Allelopathy in sustainable agriculture and forestry. Springer, New York, NY

Acknowledgements

Although my research interests in allelopathy have been a primary focus for most of my academic career, I did take several excursions into other research areas (e.g., air pollution biology, and salt marsh ecology) before returning full time to the subject matter of allelopathy. In retrospect these excursion turned out to be extremely beneficial to my understanding of stress physiology and ecosystem biology, important insights needed when studying plant–plant allelopathic interactions. My teaching of beginning and advanced undergraduate botany courses and graduate courses in plant physiology, ecology, plant physiological ecology, and root ecology also proved to be invaluable in my pursuit of understanding the mechanisms of plant–plant allelopathic interactions by providing me with an opportunity to develop a much more in-depth appreciation of plant morphology, anatomy, physiology, and population biology, and soil physics, chemistry and microbiology.

Equally as important as a solid understanding of plant, microbial, and soil biology was an appreciation of the scientific method. The importance of the scientific method as a tool for studying biological systems was instilled within me by EL Rice, my PhD mentor at The University of Oklahoma, and was reinforced by my teaching of botany courses using the Socratic Method at both the University of Oklahoma and at North Carolina State University.

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Abbreviations

ACT	Basal medium for actinomycetes
CAF	Caffeic acid
C-clover	Crimson clover
CFU	Colony-forming units
C/N	Carbon/nitrogen ratio
DBW3	EDTA extraction of soil at room temperature and soil extraction ratio
	of 1:100
DTPA	Diethylenetriaminepentaacetic acid
EDTA	Ethylenediaminetetraacetic acid
FER	Ferulic acid
GUE	Sodium hydroxide extraction of soil at room temperature and soil
	extraction ratio of 1:1 (GUE2) or at 121°C and soil extraction ratio
	of 1:43 (GUEN)
GLM	General linear model
GLU	Glucose
HPLC	High performance liquid chromatograph
kv	kilovolts
MEOH	Methanol
MES	2-(N-morpholino) ethanesulfonic acid
mOsm	milliosmoles
NLIN	Non linear
OMe	Methoxy
PEG	Polyethylene glycol
PPFD	Photosynthetic photon flux density
PCO	<i>p</i> -Coumaric acid
PDMS	Polydimethylsiloxane
РОН	<i>p</i> -Hydroxybenzoic acid
PRO	Protocatechuic acid
PVP	Polyvinylporrolidone
RCM-100	Radical Pak cartridge
R	Root
R + S	Root plus shoot

S	Shoot
S-clover	Subterranean clover
SIN	Sinapic acid
SYR	Syringic acid
VAN	Vanillic acid

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2.21	Concentrations for one to a mixture of four phenolic acids	
	required for a 30% inhibition of mean absolute rates of leaf	
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