Potential Allelopathic Effects of Jerusalem Artichoke (Helianthus tuberosus) Leaf Tissues

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Potential Allelopathic Effects of Jerusalem Artichoke (*Helianthus tuberosus*) Leaf Tissues

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Jerusalem artichoke has been reported to colonize several ecological niches and agronomic crops in southern Europe. This plant is also of interest because of its high biomass production and its potential to produce ethanol for biofuel. Allelopathy may be an advantageous trait in Jerusalem artichoke under cultivation, as it potentially reduces weed interference with the crop, theoretically allowing a reduction of mechanical or chemical input required for weed management. However, this trait may also be unfavorable if other crops are cultivated in rotation with Jerusalem artichoke or in areas infested by this species. The aim of this study was to investigate the sensitivity of selected diverse crops (wheat, lettuce, corn, tomato, rice, and zucchini) and weeds (barnyardgrass, black nightshade, common lambsquarters, common purslane, large crabgrass, and pigweed) to the presence of Jerusalem artichoke dried leaf tissues in laboratory experiments performed under controlled conditions. The simulated soil incorporation of different Jerusalem artichoke residues (four cultivars and a weedy population) was carried out in a series of laboratory and greenhouse experiments. Jerusalem artichoke reduced the radicle growth of seedling lettuce (60%), tomato (30%), large crabgrass (70%), and barnyardgrass (30%), whereas total germination of these species was less affected. Sensitivity to Jerusalem artichoke residues was species dependent; germination and initial growth of corn were not affected, whereas winter wheat, lettuce, tomato, rice, and zucchini seedlings were more sensitive to residue presence. Our experiments show that both wild and cultivated decomposing Jerusalem artichoke residues, particularly leaves and stems, possess phytotoxic potential. Additional field experimentation remains to be conducted to determine if allelopathy in the field contributes to its invasibility.

Nomenclature: Jerusalem artichoke, *Helianthus tuberosus* L.; barnyardgrass, *Echinochloa crus-galli* (L.) Beauv. ECHCG; black nightshade, *Solanum nigrum* L. SOLNI; common lambsquarters, *Chenopodium album* L. CHEAL; common purslane, *Portulaca oleracea* POROL; corn, *Zea mays* L.; large crabgrass, *Digitaria sanguinalis* (L.) Scop. DIGSA; lettuce, *Lactuca sativa* L.; pea, *Pisum sativum* L.; redroot pigweed, *Amaranthus retroflexus* L. AMARE; rice, *Oryza sativa* L.; tomato, *Lycopersicon esculentum* Mill.; wheat, *Triticum aestivum* L.; zucchini, *Cucurbita pepo* L.

Key words: Phytotoxicity, residue degradation, crop rotation, plant invasion.

Ha sido reportado que el Topinambur coloniza varios niquio ecológicas y cultivos agronómicos en el sur de Europa y especialmente en Italia. Esta planta es de interés también, por su elevada producción de biomasa y su potencial de producir etanol para biocarburantes. La alelopatía puede ser una característica vantajosa Topinambur cultivado, porque reduce potencialmente la interferencia de las malezas con los cultivos, y permite teóricamente una reducción de los aportes mecánicos y/o químicos necesarios para el manejo de las malezas. Sin embargo, esta característica puede ser también desfavorable si otros cultivos se manejan en rotación con el Topinambur o en áreas infestadas por esta especie. El objetivo de este trabajo fue de investigar la sensibilidad de algunos cultivos (trigo, lechuga, maíz, tomate, arroz y calabacín) y de algunas malezas (*Echinochloa crus-galli*, *Solanum nigrum*, *Chenopodium album*, *Portulaca oleracea*, *D. sanguinalis* y *Amaranthus retroflexus*) frente a la presencia de tejidos foliares secos de Topinambur, en un experimento de laboratorio realizado en condiciones controladas. La incorporación simulada de diferentes residuos de Topinambur en el suelo (4 cultivares y una populación de maleza) se realizó a través de series de experimentos de laboratorio y de invernadero. El Topinambur redujo el crecimiento radical de las plántulas de lechuga (60%), tomate (30%), *D. sanguinalis* (70%) y *Echinochloa crus-galli* (30%), mientras que la germinación total de estas especies ha sido menos afectada. La sensibilidad a los residuos de Topinambur fue especie dependiente; la germinación y el crecimiento inicial del maíz no han sido afectados, mientras que las plántulas de trigo, lechuga, tomate, arróz y calabacín fueron más sensibles a la presencia de los residuos. Nuestro experimento muestra como los residuos decompuestos de ambos Topinambur, cultivados y selváticos, particularmente de hojas y tallos, tienen un potencial fitotóxico. Suplementarios experimentos de campo deben ser conducidos para determinar si la alelopatía en campo contribuye a la invasibilidad del Topinambur a través de Italia.

Allelopathy, the suppressive activity of one plant species on neighboring plants by the release of toxic compounds (Molisch 1937), has had a long history of study among ecologists. Much of the early work on allelopathy was not particularly rigorous, and an influential monograph review of Harper (1964) convinced many potential researchers that chemical interactions between plants were not a profitable field of study. However, more recent and rigorous studies have demonstrated that allelopathic compounds can play an important role in the determination of plant diversity (Callaway et al. 2003), dominance, succession, adaptation of natural vegetation, and on plant yield (Orr et al. 2005). The incorporation of allelopathic substances as a part of an agricultural management program, through the use of a

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rotational or cover crop, may also have a positive effect on the environment, and is often utilized by organic producers who wish to reduce potential use of synthetic herbicides, fungicides, and insecticides (Vivanco et al. 2004; Weston 1996). A more negative aspect of allelopathy is the potential production of allelochemicals by nonnative invasive species that adversely affect native communities (Vivanco et al. 2004). Invasive plants, including noxious weeds in particular, may influence other species through competition, by altering the ecosystem processes, or through the release of potent inhibitors of plant growth known as allelochemicals. In this scenario, native plants may not have the ability to detoxify or tolerate new molecules produced and released by a nonnative invader that has not coevolved in the same habitat (Hua et al. 2005).

Another issue of concern voiced by researchers working on allelopathy is that field experiments to prove the presence of allelopathic effects are difficult if not impossible to design and conduct. In addition, many laboratory bioassays do not adequately predict the growth responses observed at field scale. In fact, it is difficult to design a bioassay that can be used profitably to examine growth responses uniformly across all species. Therefore when assessing allelopathic potential, phytotoxicity and growth response should potentially be evaluated through the use of multiple experiments and bioassay systems.

Despite the problems in studying and defining allelopathic activities, modes of action of allelochemicals, and their interactions in natural settings, important progress has been made to support the further use of allelopathy in agroecosystems for weed management (Weston 2005). Putnam and Duke (1974) first proposed the possibility of utilization of allelopathic crops to suppress weed growth in agricultural sites, and described the potential utilization of rotational crops, intercrops, or cover crops for practical weed control. The exploitation of allelopathic traits of an allelopathic crop may be advantageously taken into consideration for weed suppression, theoretically permitting significant input reductions for weed management. Several cases of highly suppressive crops are reported in the literature, and include both annual and perennial crops such as alfalfa (*Medicago sativa* L.), buckwheat (*Fagopyrum esculentum* Moench) (Xuan and Tsuzuki 2004), black mustard (*Brassica nigra* L.) (Xuan et al. 2004), and sunflower (*Helianthus annus* L.) (Azania et al. 2003; Leather 1983).

The suppressive ability of sunflower residues is well known, and the sensitivity of cereals seeded after this crop has largely been documented (Leather 1983). By contrast, the closely related species Jerusalem artichoke, a member of the Asteraceae family and native to North America, has not been adequately investigated concerning its allelopathic traits (Tesio et al. 2008; Vidotto et al. 2008). The species was first described at the beginning of the 1600s in botanical literature and, toward the middle portion of the same century, was introduced in Europe, where it was widely cultivated both for human consumption and as feed for livestock (Swanton et al. 1992). The popularity and economic role of Jerusalem artichoke has decreased quite remarkably in recent years, in relation to the success of alternative tuber crops such as potato. Conversely, the ease with which Jerusalem artichoke can be cultivated and propagated allowed the species to become invasive in several environments and as a significant weed of field crops (Török et al. 2003). Jerusalem artichoke is abundant in natural settings, such as riverbanks of European countries (Schnitzler et al. 2007), especially in Austria (Walter et al. 2005), Croatia (Vendula 2008), Slovakia (Fehér 2007), and Ukraine (Protopopova et al. 2006). In particular, the presence of tall dense stands of Jerusalem artichoke resulted in the reduction of native taxa in Austria because of interference, a change in succession patterns, and the formation of new vegetation types (Wadsworth et al. 2000; Walter et al. 2005). Shoots of Jerusalem artichoke can emerge from tubers buried as deep as 30 cm (Swanton and Cavers 1988), and volunteers of this invasive species may cause serious issues in crop yield and quality, as well as potentially being spread by later cultivation. For example, a 16 to 25% yield reduction in corn is reported with a density of approximately four tubers m^{-2} (Wyse and Young 1980). In soybean the presence of one, two, or four tubers m^{-2} reduced seed production by 31, 59 or 71% respectively (Wyse et al. 1986); whereas nearly 20% yield reduction has been observed in barley infested by four to six plants m^{-2} (Wall and Friesen 1989).

Our own field experimentation in Italy has shown that this noxious weed has spread throughout northern Italy in broad-acre row crops, particularly where it had been cropped in the past, or when allowed to propagate in an uncontrolled manner. Although labeled herbicides are available for control, the herbicide must translocate through the plant to its tubers to be effective. This noxious weed has become increasingly important in local broad-acre cropping sites, and if left unchecked establishes dense monocultural stands over time (Tesio, unpublished data). Besides developing conventional management strategies for this invasive weed, this research project was therefore designed to evaluate the potential phytotoxic effects of Jerusalem artichoke upon important succeeding crops common in field rotations. Experiments were performed in the laboratory and greenhouse in the United States and Italy. Using controlled greenhouse and laboratory conditions, we assessed the impact of artichoke genotype upon the germination and growth behavior of several crop and weed species after soil incorporation of dried residues of Jerusalem artichoke. We also attempted to simulate common field conditions by performing greenhouse studies in a controlled environment to monitor impacts of artichoke residues upon plant growth and residue decomposition in a simulated planting. These preliminary experiments provide the basis for additional work that is currently being conducted in laboratory and field settings to identify purported allelochemicals in Jerusalem artichoke, and determine the potential for longer-term allelopathic interference in field studies in northern Italy.

Materials and Methods

Plant Material. Multiplication of all vegetative material compared in the studies outlined below was conducted in a series of collaborative experiments performed at Cornell University's glasshouses located in Ithaca, NY in 2005 to 2006. Tubers of wild *H. tuberosus* L. (hereafter indicated as "Italian" population) were collected during August 2005 in heavily infested corn fields in northwestern Italy. In addition, tubers of cultivated varieties 'Fuseau', 'Red Fuseau', and 'Stampede' were purchased in early 2006 from Ronninger Potato Farm LLC,[1] whereas tubers of the hybrid variety 'Stampede Hybrid' were obtained from Sharon's Natural Gardens[2] (Delmar, DE) in an attempt to compare the potential phytotoxic activity of cultivated and naturally occurring wild Italian artichokes. After receiving all tuber genotypes, tubers were individually transplanted into plastic pots (20-cm diam) filled with commercial potting media (Metromix 360)[3] in March 2006. Pots were placed in a greenhouse maintained at daily temperatures of 23 to 30 C, with supplemental metal halide lighting of 12 h per day applied only in fall/winter months as needed. Plants were watered overhead as needed and fertilized as needed with soluble fertilizer (N–P–K 21–5–20). Jerusalem artichoke shoots were harvested periodically (generally on a monthly basis) by cutting stalks 10 cm above the soil surface, and selecting healthy individuals. The leaves were immediately separated from the stalks and dried in open trays in the laboratory drying oven at 35 C. Dried material was stored in tightly closed plastic containers until use to maintain dryness. Weed seeds used were purchased in early 2006 from Herbiseed[4] and stored at +4 C in plastic containers.

Laboratory Experiment. Allelopathic potential of the Jerusalem artichoke genotypes was evaluated in a series of laboratory experiments performed at Cornell University from June to August 2006. Inhibitory potential of dried artichoke leaf tissue was assessed in terms of impact upon seed germination and radical and hypocotyl elongation of indicator species. The experiment was conducted using the cultivars Fuseau, Red Fuseau, Stampede Hybrid, and Stampede and the wild Italian population, using square plastic petri dishes that contained a mixture of soil and plant residues, as well as indicator seedlings in a modified Parker bioassay (Weston 2005). Field soil, Chenango silt loam, fine (Psamentic halpludalf, fine, mixed, mesic) was collected at the Cornell Bluegrass Lane Turfgrass Research Farm (Ithaca, NY), and was air-dried, sifted, and combined with fine silica sand (1 : 1 v/v) for use as the experimental substrate. Sand was added to the field soil to allow for increased water permeability during the preparation of the bioassay. One hundred grams of the dry soil mixture was placed in 100 by 100 by 15 mm^2 petri dishes initially. Soil was then topped with varying amounts of chopped artichoke leaf residue (0.5, 1, or 1.5 g), and an additional 50 g of soil mixture was then layered over the residue. Dishes were moistened with 35 ml of deionized water and a square piece of filter paper[4] was placed on the soil surface of each dish. The control treatment consisted of inert prewashed paper toweling (1.0 g) cut into 1.5 mm^2 pieces added to the soil mixture. Large crabgrass, barnyardgrass, lettuce (cv. Meraviglia d'inverno), and tomato (cv. Marmande) were used as indicator species in all treatments. Ten seeds of each of the four indicator species were uniformly placed in two separate but parallel rows on the surface of the filter paper. Dishes were taped shut to maintain moisture and encourage seed/residue contact and were stored vertically at ambient room temperature of 26 C for 6 d in a germination box to promote downward root growth.

Table 1. Main physical and chemical properties of the soil substrate used in the study.

Parameter	Value	Parameter	Value
Coarse sand (%)	7	Organic matter (%)	1.20
Fine sand (%)	61	P_2O_5 Olsen (mg kg^{-1})	21.40
Coarse silt (%)	9	K_2O exchangeable (mg kg^{-1})	134.40
Fine silt (%)	18	N total (%)	0.11
Clay (%)	5	C/N ratio	6.30
Gravel (> 2 mm) (%)	Absent	Bulk density	1.40
pH (in H_2O; 1 : 2.5)	7.6	Field capacity (%)	20.30
Organic carbon (%)	0.90	Welting point (%)	5.20

Total germination was assessed by determining daily the number of germinated seeds throughout the experiment, and hypocotyl and radical length were recorded after 6 d. The experiment was arranged as a completely randomized design with three replicates, and the study was conducted on two separate dates. Experimental results were analyzed separately for each species, but results were combined over runs.

Greenhouse Experiment. Greenhouse experiments were also conducted from September 2005 to February 2006 in the experimental glasshouse of the Department Agroselviter, Università degli Studi di Torino (Italy), under temperatures varying from 15 to 25 C. Containers (8 by 8 cm^2, 8-cm height) were filled with two different soil substrates that included silica sand or soil collected at the experimental research station Tetto Frati located at Carmagnola, Italy. Soil characteristics are reported in Table 1. To each pot, 1.28 g of powdered Jerusalem artichoke population Italian dry leaves was added and thoroughly mixed, corresponding to 2 t ha^{-1} of dry residues. The amount used corresponds to an estimated quantity of dried residues left in field experiments after the harvest of tubers, and it was similar to the rate used in experiments with other allelopathic species reported by the literature (DongZhi et al. 2004a,b; Hong et al. 2004; Khanh et al. 2005; Vidotto et al. 2008). The controls were represented by pots filled with sand or soil only. The impact of Jerusalem artichoke residues was investigated by evaluation of the germination and growth of several crops and weeds. The crop species evaluated included corn (cv. Marano), green bean (*Phaseolus vulgaris* L.) (cv. Prelude), pea (cv. Meraviglia d'Italia), lettuce (cv. Meraviglia d'inverno), rice (cv. Loto), tomato (cv. Marmande), winter wheat (cv. Isengrain), and zucchini (cv. Genovese chiaro). The weeds evaluated were redroot pigweed, common lambsquarters, large crabgrass, barnyardgrass, common purslane, and black nightshade. The seeds were planted in the pots at a rate of 4 to 20 seeds depending upon the species. Immediately after seeding, the pots were watered daily with a solution containing soluble fertilizer (N–P–K 21–5–20). Afterward, the pots were watered to field capacity with deionized water. Pots were supported by use of an individual flower pot saucer beneath the pot to prevent leaching contamination from other treatments. The number of seeds per pot varied between 4 (corn, green bean, pea, rice, winter wheat, and zucchini), 6 (black nightshade, tomato, and barnyardgrass), 15 (redroot pigweed, common lambsquarters, large crabgrass, and lettuce), and 20 (common purslane). Only one indicator species was seeded in each pot.

Table 2. Laboratory experiment: effect of different concentrations of dried Jerusalem artichoke leaf tissues on total germination and shoot and root length of large crabgrass expressed as a relative percentage of the control.

Rate of dried tissue (g plate^{-1})	Cultivar	Total germination (%)	Shoot length (%)	Root length (%)
0.5	Italian	77.8 ± 6.41	114.9 ± 9.32	90.8 ± 2.78
	Fuseau	79.2 ± 13.21	14.7 ± 2.79**	8.0 ± 3.16**
	Red Fuseau	109.1 ± 0.00	87.8 ± 13.50	93.6 ± 2.41
	Stampede Hybrid	118.2 ± 12.03	87.4 ± 26.62	65.3 ± 9.57
	Stampede	103.7 ± 9.04	66.5 ± 17.49	45.2 ± 4.97*
1.0	Italian	48.1 ± 13.35	73.9 ± 13.87*	62.9 ± 19.28*
	Fuseau	61.6 ± 4.40**	15.6 ± 5.48**	5.4 ± 5.40**
	Red Fuseau	113.6 ± 4.54	74.7 ± 16.06	89.9 ± 15.48
	Stampede Hybrid	109.1 ± 7.87	72.8 ± 15.24	36.2 ± 4.30*
	Stampede	64.5 ± 20.62	26.7 ± 11.48*	21.0 ± 6.99*
1.5	Italian	70.4 ± 3.70**	86.7 ± 18.36	59.0 ± 11.55**
	Fuseau	22.0 ± 4.40**	13.7 ± 5.48**	4.9 ± 4.90**
	Red Fuseau	113.6 ± 9.09**	54.5 ± 20.53**	48.4 ± 12.29**
	Stampede Hybrid	90.9 ± 12.02	29.1 ± 8.66*	18. 2 ±4.96*
	Stampede	27.3 ± 7.15*	5.6 ± 1.26**	14.0 ± 0.00*

*, significant differences from the control treatment with P ≤ 0.05; **, significant differences from the control treatment with P ≤ 0.01.

Seeds of barnyardgrass were scarified for 40 min in concentrated sulfuric acid to treat for potential seed dormancy. Greenhouse temperature during the experiment averaged 18.7 C. Pots were arranged on greenhouse benches in a completely randomized design, with four replicates, and rotated every week to minimize spatial variation. The experimental unit was the pot. The experiment was then repeated in time. Natural light was supplemented by metal halide lamps adjusted to produce 14-h day length, delivering about 55 µmol s^{-1} m^{-2}. Germination percentage, seedling height, and shoot dry weight were determined 20 d after seeding (DAS) (Macías et al. 2004) for corn, green bean, lettuce, pea, winter wheat, and zucchini, and 30 DAS for all the other species.

Statistical Analysis. Relative values, as percentage of the values recorded in the controls, were calculated for all data of both greenhouse and laboratory experiments, and a *t* test was performed to evaluate the effects of Jerusalem artichoke dried residues in comparison with control values.

The severity of the inhibitory effects caused by the tested cultivars was assessed with the total inhibition index. Total inhibition index is the ratio of the area of inhibition on the total area. The area of inhibition was obtained using the "trapezium rule" (Brown and Stewartson 1983; Burden and Faires 1988) to estimate the integral of the response of the tested species at the quantities of dried residues used (0, 0.5, 1, 1.5 g), using 100% as upper limit of development. For each cultivar, the response of both root and shoot growth of all tested species was pooled. ANOVA and a post hoc LSD test were performed to separate means using the software SPSS (version 16).[5]

Results and Discussion

Laboratory Experiment. Effects on seed germination and first seedling growth of the indicator species varied from stimulation to considerable inhibition, especially when high rates of dried leaf tissue were utilized in laboratory experiments. Plant growth was affected by the addition of Jerusalem artichoke dried leaf material and varied according to the test species and with the genotype of the source material used. Fuseau was observed to be, on average, the most toxic cultivar in terms of impact upon total germination, as it caused significant inhibition at the lowest rate of residue incorporation (0.5 g plates^{-1}). For example, large crabgrass final germination recorded at 1.5 g plate^{-1} was not affected with Red Fuseau, showing a value significantly higher than that recorded in the control (Table 2), whereas Fuseau caused a reduction of about 38 and 78% at 1 and 1.5 g plate^{-1}, respectively. Seedling growth of large crabgrass was also strongly affected by Fuseau, Italian, and Stampede, even at the lowest amount of dried tissue incorporated with the cultivar Fuseau. All cultivars showed an effect on large crabgrass radical elongation, with inhibition greater than 40% at the highest rate of residue incorporation.

None of the five tested cultivars significantly inhibited the germination of barnyardgrass at 0.5 and even 1 g plate^{-1}, with the exception of Stampede reducing germination by approximately 20% (Table 3). Significant effects compared with control treatment in terms of seedling growth were observed at the highest rate of residues for all cultivars, and 1 g plate^{-1} in the case of Fuseau. Root length was significantly affected by all cultivars at 1.5 g plate^{-1}, and with Fuseau, Stampede Hybrid, and Stampede at 1 g plate^{-1}, and Stampede Hybrid at 0.5 g plate^{-1}.

Although lettuce is often considered highly sensitive to allelopathic substances, none of the cultivars inhibited germination percentage of lettuce at the lower incorporation rate, and only one cultivar (Fuseau) affected this index at incorporation of 1 g plate^{-1}. At the highest incorporation rate of dried leaf tissue, only Stampede did not show a reduction of germination percentage (Table 4). Shoot and root growth were more affected than germination, as radical elongation, in particular, was reduced by about 50% by 1 g plate^{-1} of dried leaf residues, and reduced by more than 78% at 1.5 g plate^{-1} with all tested cultivars.

On average, tomato was the most sensitive indicator species to Jerusalem artichoke dried leaf tissues. For example, no germination was observed with the lowest amount of Fuseau residue incorporated (Table 5), whereas Stampede reduced germination by 70% and 90% at 0.5 g plate^{-1} and 1 g

Table 3. Laboratory experiment: effect of different concentrations of dried Jerusalem artichoke leaf tissues on total germination and shoot and root length of barnyardgrass expressed as a relative percentage of the control.

Rate of dried tissue (g plate^{-1})	Cultivar	Total germination (%)	Shoot (%)	Root (%)
0.5	Italian	88.1 ± 5.66	111.5 ± 5.78	111.1 ± 15.75
	Fuseau	88.5 ± 11.53	75.6 ± 10.39	100.6 ± 18.80
	Red Fuseau	70.2 ± 14.80	115.1 ± 4.53*	110.6 ± 13.22
	Stampede Hybrid	81.2 ± 7.57	78.2 ± 11.89	60.7 ± 8.47**
	Stampede	103.7 ± 9.04	66.5 ± 17.49	45.2 ± 4.97
1.0	Italian	79.4 ± 9.93	85.6 ± 9.17	81.5 ± 12.74
	Fuseau	85.4 ± 14.01	47.0 ± 13.66*	60.5 ± 13.28*
	Red Fuseau	74.6 ± 8.35	89.2 ± 6.81	99.5 ± 18.74
	Stampede Hybrid	79.0 ± 8.02	92.6 ± 5.85	49.2 ± 16.27*
	Stampede	93.3 ± 17.64	65.0 ± 20.98	33.1 ± 16.42*
1.5	Italian	74.2 ± 8.02**	65.8 ± 6.91**	56.4 ± 11.38**
	Fuseau	72.4 ± 8.64**	46.0 ± 11.48**	67.9 ± 10.40**
	Red Fuseau	81.6 ± 10.73**	79.8 ± 8.72**	76.5 ± 12.65**
	Stampede Hybrid	87.7 ± 6.07**	68.7 ± 8.65**	34.9 ± 10.86**
	Stampede	109.7 ± 5.78**	67.7 ± 14.13**	35.1 ± 8.80**

*, significant differences from the control treatment with P ≤ 0.05; **, significant differences from the control treatment with P ≤ 0.01.

Table 4. Laboratory experiment: effect of different concentrations of dried Jerusalem artichoke leaf tissues on total germination and shoot and root length of lettuce expressed as a relative percentage of the control.

Rate of dried tissue (g plate^{-1})	Cultivar	Total germination (%)	Shoot (%)	Root (%)
0.5	Italian	103.1 ± 4.24	75.8 ± 15.22	73.1 ± 14.33
	Fuseau	83.5 ± 9.42	65.4 ± 20.17	47.7 ± 22.00
	Red Fuseau	70.2 ± 5.27	115.1 ± 13.71*	110.6 ± 6.85**
	Stampede Hybrid	105.7 ± 3.26	51.8 ± 6.41**	48.5 ± 13.74*
	Stampede	100.0 ± 3.45	59.0 ± 27.72	37.0 ± 8.75**
1.0	Italian	95.7 ± 2.97	58.0 ± 15.19*	57.2 ± 11.10*
	Fuseau	72.5 ± 9.74*	43.7 ± 12.52**	18.2 ± 8.41**
	Red Fuseau	87.8 ± 12.99	46.2 ± 8.33**	48.6 ± 8.31**
	Stampede Hybrid	93.7 ± 6.91	38.2 ± 5.00**	27.2 ± 7.10**
	Stampede	93.1 ± 5.97	42.2 ± 9.79**	18.2 ± 3.77**
1.5	Italian	78.4 ± 6.19**	14.8 ± 8.52**	21.8 ± 6.51**
	Fuseau	71.0 ± 10.64**	18.5 ± 5.87**	16.3 ± 7.86**
	Red Fuseau	79.9 ± 7.14**	37.8 ± 18.15**	36.6 ± 11.21**
	Stampede Hybrid	59.4 ± 11.23**	15.5 ± 6.26**	14.1 ± 0.69**
	Stampede	100.0 ± 3.45	33.1 ± 9.50**	15.3 ± 3.42**

*, significant differences from the control treatment with P ≤ 0.05; **, significant differences from the control treatment with P ≤ 0.01.

Table 5. Laboratory experiment: effect of different concentrations of dried Jerusalem artichoke leaf tissues on total germination and shoot and root length of tomato expressed as a relative percentage of the control.

Rate of dried tissue (g plate^{-1})	Cultivar	Total germination (%)	Shoot (%)	Root (%)
0.5	Italian	95.8 ± 11.02	97.4 ± 27.04	98.5 ± 28.27
	Fuseau	0.0 ± 0.00**	0.0 ± 0.00**	0.0 ± 0.00**
	Red Fuseau	122.2 ± 5.55	33.8 ± 5.83	75.1 ± 1.32
	Stampede Hybrid	88.9 ± 14.70	49.0 ± 16.33	53.8 ± 18.41
	Stampede	30.0 ± 8.66**	35.2 ± 11.18*	44.5 ± 4.69*
1.0	Italian	83.3 ± 4.16*	100.7 ± 42.30	90.9 ± 35.50
	Fuseau	4.4 ± 4.40**	1.4 ± 1.36**	0.0 ± 0.00**
	Red Fuseau	77.8 ± 24.22	28.2 ± 14.08	61.3 ± 22.65
	Stampede Hybrid	77.8 ± 22.2	40.8 ± 8.17	40.5 ± 15.98
	Stampede	10.0 ± 10.00**	21.0 ± 11.09**	38.4 ± 10.85*
1.5	Italian	82.0 ± 7.00**	56.9 ± 19.86**	80.5 ± 14.76**
	Fuseau	0.0 ± 0.00**	0.0 ± 0.00**	0.0 ± 0.00**
	Red Fuseau	50.0 ± 9.62**	27.2 ± 16.56*	49.4 ± 9.37**
	Stampede Hybrid	72.2 ± 5.55**	25.6 ± 5.17*	22.3 ± 2.77*
	Stampede	10.0 ± 10.00**	8.4 ± 8.38**	18.6 ± 9.56*

*, significant differences from the control treatment with P ≤ 0.05; **, significant differences from the control treatment with P ≤ 0.01.

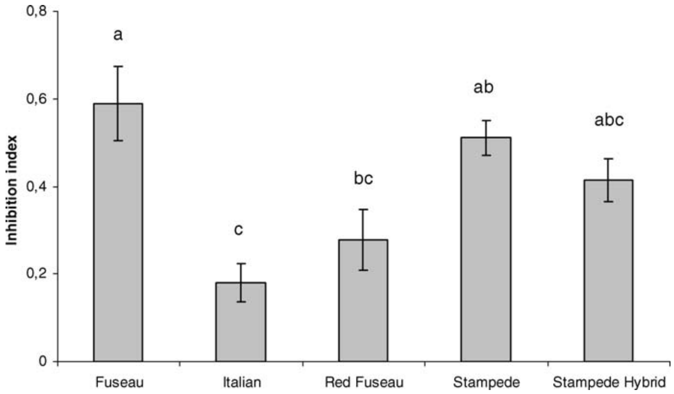

Figure 1. Laboratory experiment: inhibition index (0 = no inhibition; 1 = complete inhibition) calculated for each cultivar. Bars refer to standard error of the mean (n = 8). Means followed by the same letter(s) are not significantly different (LSD test: P = 0.05).

plate^{-1}, respectively, indicating significant variation in response that was genotype dependent. Cultivar Stampede also inhibited tomato shoot (from 65 to 95%) and root growth (from 56 to 81%) at the 0.5g plate^{-1} rate of incorporation.

Considering the overall effect on shoot and root growth, Fuseau, Stampede, and Stampede Hybrid could be described as the most phytotoxic or potentially allelopathic cultivars, even if the latter was not significantly different from the naturalized weedy population Italian (Figure 1). The inhibition index observed for the cultivar Fuseau was roughly one–third of that recorded for Italian. Somewhat surprisingly, the cultivated varieties of Jerusalem artichoke were considerably more phytotoxic than the wild Italian artichoke, even when cultivated under similar conditions in an Ithaca glasshouse. The variation in phytoxicity is relatively large and cultivar or biotype dependent.

Greenhouse Experiment. No differences in total germination in comparison with the control were observed across all crops seeded in sand media. However, in soil, the presence of Jerusalem artichoke dried residues resulted in 36% reduction of the germination of zucchini, lettuce, and rice (Figure 2). This response may be explained with the more rapid germination observed in sand media as compared with soil, which did not permit one to observe any significant allelopathic effect over time in this substrate. In comparison with sand media, the germination in soil was, on average, reduced in overall percentage and over time. Among the crops evaluated, lettuce showed the highest sensitivity to Jerusalem artichoke residues. Seedling growth of the largest seeded indicator, corn, was not affected in either the sand or soil media treatments. The other monocotyledonous crops grown in sand, such as winter wheat and rice, were affected over time in terms of plant height, and also plant weight in the case of rice. In soil pots, all growing parameters of winter wheat were reduced by the presence of dried residues. Germination of rice in soil media was also lower than that recorded in the control treatment by approximately 46%. Tomato plant weight was reduced by 66% and 55% in sand and soil respectively, and both substrates also showed significant reductions in plant height.

In both substrates, no significant effects on germination percentage of broadleaf weeds were observed (Figure 3). In

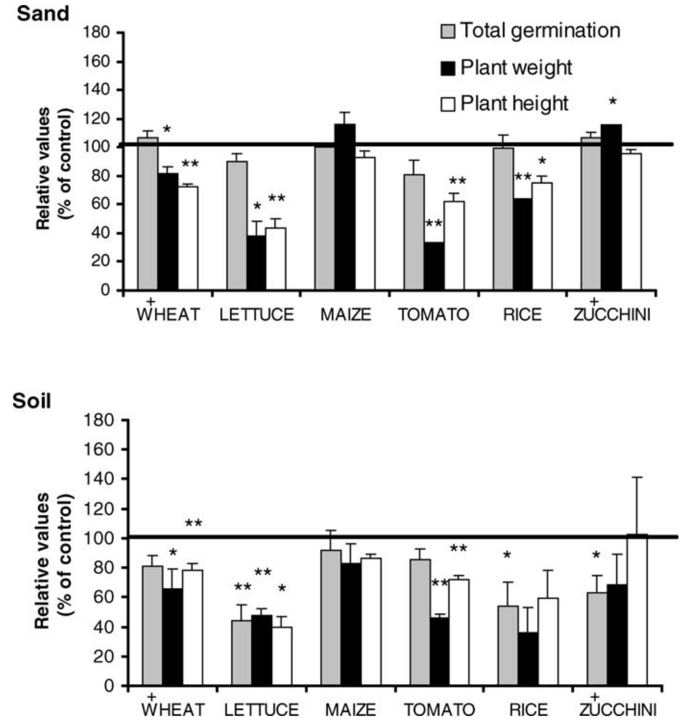

Figure 2. Greenhouse experiment: response of weed species to the presence of 2 t ha^{-1} of dried residues of Jerusalem artichoke. Bars represent the standard errors. *, significant differences from the control (black line) with P $\leq$ 0.05 or ** with P $\leq$ 0.01. Significant differences between sand and soil substrates within the same parameter and species are marked with + for P $\leq$ 0.05.

redroot pigweed, large crabgrass, and common purslane, the addition of Jerusalem artichoke dried residues to the growing media, both in sand or soil substrates, resulted in a significant reduction of seedling height and weight.

In barnyardgrass, germination percentage was significantly enhanced in the case of sand, whereas it was strongly reduced (by about 40%) in the case of soil media treatment. In general, individual plant weight was the parameter most strongly affected by the presence of the Jerusalem artichoke residue.

The allelopathic potential of the *Helianthus* genus has been widely studied, especially with respect to the common sunflower, on which an important amount of information is available regarding its ability to reduce weed growth. Only a few studies, however, have been reported on the allelopathic potential of the related perennial species, Jerusalem artichoke (Saggese et al. 1985; Tesio et al. 2008; Vidotto et al. 2008).

In these experiments, effects of various amounts of Jerusalem artichoke dried residue produced variable results with respect to seed germination and seedling growth of different indicator species. Although some stimulation was recorded, inhibition of growth was more commonly observed, especially when dried residues were evaluated at high rates of soil incorporation.

In allelopathic studies, several factors can reduce the availability of allelochemicals in the leachates or in the rhizosphere, including adsorption by organic matter and microbial degradation (Reigosa et al. 1999). For this reason, different treatments addressing the impact of soil type were introduced in the study, particularly the evaluation of soil or sand in the greenhouse experiment and the use of different

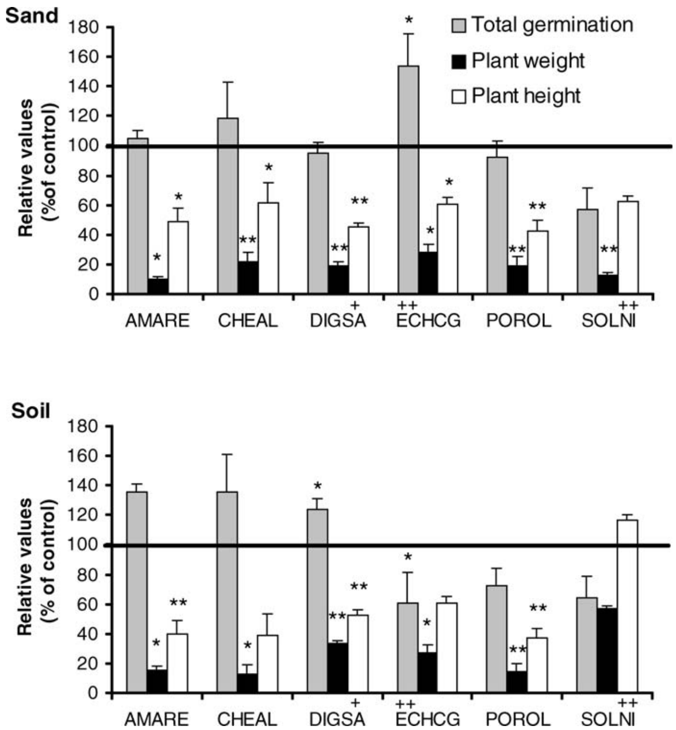

Figure 3. Greenhouse experiment: response of crop species to the presence of 2 t ha^{-1} of dried residues of Jerusalem artichoke. Bars represent the standard errors. *, significant differences from the control (black line) with $P \leq 0.05$ or ** with $P \leq 0.01$. Significant differences between sand and soil substrates within the same parameter and species are marked with + for $P \leq 0.05$ and with ++ for $P \leq 0.01$.

cultivars of Jerusalem artichoke as source of residue material. The Parker bioassay method adopted in the laboratory study allows one to simulate the constant release of allelochemicals into soil caused by tissue degradation over time after incorporation. The presence of soil in this bioassay allows one to create a more realistic simulation of the field environment compared with the experiments carried out with the aqueous extracts in agar or petri dishes, in which the toxic compounds are often present in greater quantity and availability for uptake.

The laboratory bioassay confirmed the allelopathic activity of Jerusalem artichoke on the indicator species, with activity also observed on barnyardgrass, large crabgrass, lettuce, and tomato in the greenhouse experiment. Although the various cultivars of Jerusalem artichoke exhibited allelopathic effects, no statistically significant differences were observed among the cultivated varieties (Fuseau, Red Fuseau, Stampede, and Stampede Hybrid) and the weedy population (Italian). Interestingly, the domestication of Jerusalem artichoke for agricultural uses is apparently not affecting allelopathic severity, whereas long-term selection in cereal species has led to a loss of competitive ability or allelopathy traits (Bertholdsson 2004). Among the tested cultivars, Fuseau showed the highest phytotoxicity, followed by the cultivars Stampede and Stampede Hybrid.

A stronger allelopathic effect was anticipated in pots containing sand than in pots filled with soil in the greenhouse experiment; however, the opposite was observed. These results may have been associated with the short duration of the greenhouse experiment, or the ability of the test crops to germinate more quickly and uniformly in the sand media vs. the field media. Furthermore, decomposition and availability of allelochemicals due to decomposition could have been a factor. Field soils generally contain larger numbers of viable soil microbial organisms than sand media. A greater microbial activity may account for enhanced degradation of artichoke residues in the field soil, providing a more sustained release of allelochemicals over time, leading to greater impacts upon plant growth. Although we cannot rule out the possibility of other microbial interactions, our experimental units appeared healthy, except at highest rates of artichoke incorporation. A field study established over a longer period may provide more insight into this effect. The germination of indicator species in the sand treatment was generally higher, and similar to the control, in comparison with that observed in the field soil treatment.

In both laboratory and greenhouse experiments Jerusalem artichoke dried leaf tissues were more active in influencing seedling growth than the germination process itself. The effects of Jerusalem artichoke dried residues upon seedling germination and growth reported in this study may partially explain its ecological and agronomical advantage in natural and agricultural environments. The rapid spread of Jerusalem artichoke across Europe and Italy may be attributed to this allelopathic effect as well as other factors such as its ability to reproduce vegetatively by tubers (Schittenhelm et al. 1996). In highly competitive environments, even small delays in germination and emergence pattern of a species or a community may give a competitive species the ability to benefit over a less competitive neighbor, and a new equilibrium within the plant communities may be established after a period of adaptation. In the wild, Jerusalem artichoke has proven to be a noxious weed in a variety of crops and when cultivated in high density, it may also present a strong competitive advantage due to the production of great quantities of residue. Dense stands of Jerusalem artichoke can also affect succeeding crops, especially by affecting the establishment of a less competitive crop such as tomato.

The introduction of Jerusalem artichoke in agroecosystems as an edible crop and also as an energy crop for ethanol production raises several questions related to the potential of this weedy species to escape from cultivation, and its utilization as a "living" rotational crop. In addition, problems with potential eradication of this increasingly invasive species may also occur because of its perennial growth habit and ability to rapidly spread in the field by tuber production.

Given the potential of Jerusalem artichoke to reduce crop growth and yields, it is clearly important to determine if reductions are related to resource-based competition or also to allelopathy. With these considerations in mind, this study suggests that particular attention must be paid to the residue management of Jerusalem artichoke, especially in view of impact on rotational crops. In the greenhouse experiment, the amount of leaf tissue used was equivalent to a fairly high aboveground biomass production that can be achieved with a cultivation of Jerusalem artichoke; thus at the greenhouse pot level, we attempted to recreate a possible field situation in which crop residues are incorporated into the soil after tuber harvest and a successive crop is planted. In a hypothetical use of this crop for tuber production, the plant residues may be incorporated in the soil or left on the ground to take advantage of the suppressive effects of this residue against weed establishment. In this case the sensitivity of the following crop should be taken into consideration. In our studies, germination and initial growth of corn were not affected, whereas winter wheat, lettuce, tomato, rice, and zucchini were more sensitive to residue presence. However, it should be noted that in the greenhouse and laboratory studies we performed here, only the leaves, reported as the most allelopathic plant part (Khanh et al. 2005), were used. Further studies evaluating the presence of artichoke roots and tubers in field settings are required to fully determine the total impact of this invasive species upon weed and crop establishment in successive cropping systems.

Sources of Materials

[1] Ronninger Potato Farm LLC, 12101 2135 Rd., Austin, CO 81410.

[2] Sharon's Natural Gardens, 8887 Blackbird Rd., Delmar, DE 19940.

[3] Metromix 360, SUNGRO Horticulture, 15831 NE 8th Street, Suite 100, Bellevue, WA 98008.

[4] Herbiseed, New Farm, Mire Lane, West End, Twyford RG10 0NJ, UK.

[5] SPSS version 16.0 for Windows, SPSS INC., 233 South Wacker Drive, Chicago, IL 60606.

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Literature Cited

Azania, A.A.P.M., et al. 2003. Allelopathic plants. 7. Sunflower (*Helianthus annuus* L.). Allel. J. 11:1–20.

Bertholdsson, N. O. 2004. Variation in allelopathic activity over 100 years of barley selection and breeding. Weed Res. (Oxford) 44:78–86.

Brown, S. N. and K. Stewartson. 1983. On an integral equation of marginal separation. Siam J. Appl. Math. 43:1119–1126.

Burden, R. and J. Faires, eds. 1988. Numerical Analysis. 4th ed. Boston: PWS Publishing.

Callaway, R. M., S. C. Pennings, and C. L. Richards. 2003. Phenotypic plasticity and interactions among plants. Ecology 84:1115–1128.

DongZhi, L., E. Tsuzuki, Y. Sugimoto, D. YanJun, M. Matsuo, and H. Terao. 2004a. Allelopathic effects of aqueous *Aloe vera* leaf extracts on selected crops. Allel. J. 13:67–74.

DongZhi, L., E. Tsuzuki, D. YanJun, H. Terao, and T. D. Xuan. 2004b. Potential biological control of weeds in rice fields by allelopathy of dwarf lilyturf plants. BioControl 49:187–196.

Fehér, A. 2007. Historical reconstruction of expansion of non-native plants in the Nitra river basin (sw Slovakia). Kanitzia 15:47–62.

Harper, J. L. 1964. The nature and consequence of interference among plants. Pages 465–481 *in* Proccedings of the 11th International Conference of Genetics. The Hague, the Netherlands.

Hong, N. H., T. D. Xuan, E. Tsuzuki, H. Terao, M. Matsuo, and T. D. Khanh. 2004. Weed control of four higher plant species in paddy rice fields in Southeast Asia. J. Agron. Crop Sci. 190:59–64.

Hua, S., P. ShaoLin, W. XiaoYi, Z. DeQing, and Z. Chi. 2005. Potential allelochemicals from an invasive weed *Mikania micrantha* H.B.K. J. Chem. Ecol. 31:1657–1668.

Khanh, T. D., N. H. Hong, T. D. Xuan, and I. M. Chung. 2005. Paddy weed control by medicinal and leguminous plants from Southeast Asia. Crop Prot. 24:421–431.

Leather, G. R. 1983. Sunflowers (*Helianthus annus*) are allelopathic to weeds. Weed Sci. 31:37–42.

Macías, F. A., A. Oliveros-Bastidas, D. Marín, D. Castellano, A. M. Simonet, and J.M.G. Molinillo. 2004. Degradation studies on benzoxazinoids. Soil degradation dynamics of 2,4-dihydroxy-7-methoxy-(2*H*)-1,4-benzoxazin-3(4*H*)-one (DIMBOA) and its degradation products, phytotoxic allelochemicals from Gramineae. J. Agric. Food Chem. 52:6402–6413.

Molisch, H. 1937. Der einfluss einer pflanze auf die andere-allelopathie. Jena, Germany: Gustav Fischer Verlag Jena. 106p.

Orr, S. P., J. A. Rudgers, and K. Clay. 2005. Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. Plant Ecol. 181:153–165.

Protopopova, V., M. Shevera, and S. Mosyakin. 2006. Deliberate and unintentional introduction of invasive weeds: a case study of the alien flora of Ukraine. Euphytica 148:17–33.

Putnam, A. R. and W. O. Duke. 1974. Biological suppression of weeds: evidence for allelopathy in accessions of cucumber. Science 185:370–372.

Reigosa, M. J., A. Sanchez-Moreiras, and L. Gonzales. 1999. Ecophysiolocal approach in allelopathy. Critical Reviews in Plant Sciences 18:577–608.

Schittenhelm, S. 1996. Competition and control of volunteer Jerusalem artichoke in various crops. Journal of Agronomy and Crop Science 176:103–110.

Saggese, E., T. Foglia, G. Leather, M. Thompson, D. Bills, and P. Hoagland. 1985. Fractionation of allelochemicals from oilseed sunflowers and Jerusalem artichokes. Pages 99–112 *in* A. Thompson, ed. The Chemistry of Allelopathy: Biochemical Interactions among Plants. Washington, DC: American Chemical Society.

Schnitzler, A., B. W. Hale, and E. M. Alsum. 2007. Examining native and exotic species diversity in European riparian forests. Biol. Conserv. 138:146–156.

Swanton, C. J. and P. B. Cavers. 1988. Regenerative capacity of rhizomes and tubers from two populations of *Helianthus tuberosus* L. (Jerusalem artichoke). Weed Res. 28:339–345.

Swanton, C. J., P. B. Cavers, D. R. Clements, and M. J. Moore. 1992. The biology of Canadian weeds. 101. *Helianthus tuberosus* L. Can. J. Plant Sci. 72:1367–1382.

Tesio, F., F. Vidotto, L. A. Weston, and A. Ferrero. 2008. Allelopathic effects of aqueous leaf extracts of *Helianthus tuberosus* L. Allel. J. 22:47–58.

Török, K., Z. Botta-Dukát, I. Dancza, I. Németh, J. Kiss, B. Mihály, and D. Magyar. 2003. Invasion gateways and corridors in the Carpathian basin: biological invasions in Hungary. Biol. Inv. 5:349–356.

Vendula, Š. 2008. Invasive plant species in riverbank vegetation of water courses in the basin of the Ploucnice River. GeoScape 3:33–37.

Vidotto, F., F. Tesio, and A. Ferreo. 2008. Allelopathic effects of *Helianthus tuberosus* L. on germination and seedling growth of several crops and weeds. Biol. Agric. Hort. 26:55–68.

Vivanco, J. M., H. P. Bais, F. R. Stermitz, G. C. Thelen, and R. M. Callaway. 2004. Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. Ecol. Lett. 7:285–292.

Wadsworth, R. A., Y. C. Collingham, S. G. Willis, B. Huntley, and P. E. Hulme. 2000. Simulating the spread and management of alien riparian weeds: are they out of control? J. Appl. Ecol. 37:28–38.

Wall, D. A. and G. H. Friesen. 1989. Volunteer Jerusalem artichoke (*Helianthus tuberosus*) interference and control in barley (*Hordeum vulgare*). Weed Technol. 3:170–172.

Walter, J., F. Essl, T. Englisch, and M. Kiehn. 2005. Neophytes in Austria: habitat preferences and ecological effects. NEOBIOTA 6:13–25.

Weston, L. A. 1996. Utilization of allelopathy for weed management in agroecosystems. Agron. J. 88:860–866.

Weston, L. A. 2005. History and current trends in the use of allelopathy for weed management. HortTechnology 15:529–534.

Wyse, D. L. and F. L. Young. 1980. Jerusalem artichoke interference in corn [=maize] and soybeans. Pages 48 *in* Proceedings of the North Central Weed Control Conference. Milwaukee, WI: North Central Weed Science Society.

Wyse, D. L., F. L. Young, and R. J. Jones. 1986. Influence of Jerusalem artichoke (*Helianthus tuberosus*) density and duration of interference on soybean (*Glycine max*) growth and yield. Weed Sci. 34:243–247.

Xuan, T. D., T. Eiji, T. Shinkichi, and T. D. Khanh. 2004. Methods to determine allelopathic potential of crop plants for weed control. Allel. J. 13:149–164.

Xuan, T. D. and E. Tsuzuki. 2004. Allelopathic plants: buckwheat (*Fagopyrum* spp.). Allel. J. 13:137–148.

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