The effects of temperature on decomposition and allelopathic phytotoxicity of boneseed litter

Md. Abdullah Yousuf Al Harun*, Joshua Johnson, Md. Nazim Uddin, Randall W. Robinson

Institute for Sustainability and Innovation, College of Engineering and Science, Victoria University, Melbourne, Vic 8001, Australia

ARTICLE INFO

ABSTRACT

Decomposition of plant litter is a fundamental process in ecosystem function, carbon and nutrient cycling and, by extension, climate change. This study aimed to investigate the role of temperature on the decomposition of water soluble phenolics (WSP), carbon and soil nutrients in conjunction with the phytotoxicity dynamics of *Chrysanthemoides monilifera* subsp. *monilifera* (boneseed) litter. Treatments consisted of three factors including decomposition materials (litter alone, litter with soil and soil alone), decomposition periods and temperatures (5–15, 15–25 and 25–35°C (night/day)). Leachates were collected on 0, 5, 10, 20, 40 and 60th days to analyse physico-chemical parameters and phytotoxicity. Water soluble phenolics and dissolved organic carbon (DOC) increased with increasing temperature while nutrients like SO_4^2 and NO_3^1 decreased. Speed of germination, hypocotyl and radical length and weight of *Lactuca sativa* exposed to leachates were decreased with increasing decomposition temperature. All treatment components had significant effects on these parameters. There had a strong correlation between DOC and WSP, and WSP content of the leachates with radical length of test species. This study identified complex interactivity among temperature, WSP, DOC and soil nutrient dynamics of litter occupied soil and that these factors work together to influence phytotoxicity.

© 2015 The Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences. Published by Elsevier B.V.

Introduction

Decomposition of plant litter, a fundamental process of an ecosystem's function, is essential to carbon and nutrient cycling, and consequently, may influence climate. Research has suggested both positive (Northup et al., 1998) and negative (Xiong and Nilsson, 2001) impacts of litter decomposition on the environment. The impact of some environmental parameters such as soil quality and microorganisms on litter decomposition has been well established (Kobayashi, 2004). The mechanisms underpinning the positive impacts of litter decomposition are widely recognised and include: controlling soil erosion, preserving moisture, providing soil nutrients, reducing weed infestations, and providing habitat for soil fauna (Davies, 1988; Facelli and Pickett, 1991; Holland and Coleman, 1987; McGinnies, 1987).

However, there are negative impacts related to: the release of greenhouse gases (Schlesinger and Andrews, 2000), leaching of allelochemicals (Unger et al., 2010), physical impediment (Jones et al., 1997), reduced light penetration (Foster and Gross, 1998), and detrimental effects on beneficial soil microorganisms (Rice, 1965). Litter carbon, mineral and toxin decomposition and their potential possible positive or negative feedback on soil processes and the local plant community are controlled by the types and quantity of the litter, soil characteristics, soil microorganisms and climate, in particular temperature and rainfall (Beare et al., 1992; Hobbie, 1992, 1996; Salamanca et al., 2003; Saura-Mas et al., 2012).

In the last few decades, studies on litter decomposition have focused on carbon balance and climate change (Cramer et al., 2001; Davidson and Janssens, 2006), nutrient cycling (Flanagan

---

and Cleve, 1983), and, more recently, effects of litter on biodiversity (Harun et al., 2014; Kumar et al., 2009). Comparatively few of these recent investigations have probed the mechanisms underpinning the effects of litter on biodiversity. Litter allelopathy, although considered an important mechanism influencing plant community structure (Lodhi, 1978), has been little studied in dynamic relation to other parameters including temperature, soil carbon and nutrient content, and phytotoxicity. An et al. (2002) suggested that it is important to include both intrinsic and extrinsic factors in the study of residue allelopathy as they function interactively. There have been studies on the impacts of aerobic and anaerobic conditions on litter decomposition and phytotoxicity (Uddin et al., 2014b), however, the influence of temperature on these processes has not been investigated. Kinetic theory postulates that the constraints to decomposition that are caused by biological and chemical processes must themselves be affected by temperature (Thornley and Cannell, 2001) and other climate-related drivers. May and Ash (1990a, 1990b) suggested that allelochemicals decay over time, but only tested this under constant temperature. Likewise, temperatures that simulate those in nature have received no attention in relation to decomposition times and decomposition materials. The impact of temperature on the fate of allelochemicals remains largely unanswered even though the role of temperature and seasonal variation is critical to understanding the decomposition of allelopathic components in litter and their relative phytotoxicity (Steinsiek et al., 1982).

There has been an increasing focus on temperature in relation to soil organic matter decomposition in recognition of its importance to the global carbon cycle and the contribution of decomposition to climate change. Litter decomposition and its impact on nutrient availability and net primary production have been identified as a major driver of species diversity and richness (Shaver and Chapin, 1986). Mitchell et al. (2011) in a study on invasive species, suggested season-varied, and thus temperature related impacts on nitrogen mineralization and immobilization, soil carbon decomposition and microbial activities. Allelochemicals produced by plants may exhibit a phytotoxic effect, including effects on decomposition rates of soil organic matter, and may, in some cases impact directly on available nitrogen and phosphate content of soil organic matter (Inderjit and Mallik, 1997). Polyphenolics are the main components of plant allelochemicals that are associated with litter decomposition and nitrogen cycling mechanisms and are primarily responsible for the observed phytotoxic effects (Baldwin et al., 1983; Gosz, 1981; Inderjit, 1996; Rice, 1984).

Previous studies have suggested that allelopathy may play as important a role as competition for soil moisture, nutrients, sunlight, and space in determining plant community structure (Inderjit and Dakshini, 1994). Plant-plant negative interactions through the release of allelochemicals in the mode of volatilization (Halligan, 1975), root exudation (Liu et al., 2013; Uddin et al., 2014a), decomposition of residues in soil (Bonanomi et al., 2005), and leaching (Ens et al., 2009; Uddin et al., 2012) are well established. More specifically, plant litter may affect seed germination and seedling growth of neighbouring species (Rice, 1984). The dynamics of phytotoxicity may be either increased or decreased by the change in the composition and quantity of allelochemicals in association with litter decomposition time

(An et al., 2001). Additionally, allelochemical concentrations have been found to seasonally vary in their specific content and related phytotoxicity (Yamamoto, 1995). Allelopathins of plant litter may have direct impacts, through leaching, on plant growth (Bonanomi et al., 2005), or indirect effects by reducing soil nutrients and affecting the soil microbial community (Teuben, 1991).

Weeds under nutrient stress may produce large quantity of allelochemicals, and similarly, crops under conditions of nutrient scarcity accumulate higher amount of allelochemicals. Residues of such crops may exhibit phytotoxicity (Inderjit and del Moral, 1997). Nutrient immobilization, depletion of O_2 in the soil, toxicity of CO_2 produced in soil, and allelochemicals may, together, determine the phytotoxicity of litter on neighbouring species (de Jong and Klinkhamer, 1985; Rice, 1979). Although the allelopathic effects of plant residues have been extensively studied (Horner et al., 1988; May and Ash, 1990a, 1990b), the impact of temperature on the fate of these toxins and their phytotoxicity remain unknown. There is a need to investigate the impact that temperature has on litter decomposition and subsequent phenolic concentration, soil nutrient availability and phytotoxicity dynamics.

Boneseed (*Chrysanthemoides monilifera* subsp. *monilifera*), a Weed of National Significance in Australia and listed on the National Pest Plant Accord in New Zealand, has been identified as a major source of phytotoxic allelochemicals and a plant of serious ecological impacts on native species (Groves, 2008; Harun et al., 2014; Weiss et al., 2008). Boneseed infestations have also occurred in South Africa, USA and France (Weiss et al., 1998). Boneseed develops monocultures in areas of undisturbed native vegetation because of its prodigious potential for spread and regeneration, absence of natural enemies, competitive capacity and is seen as a major threat due to its fire hazard, economic and environmental impacts and its threat to native species (Parsons, 1973; Rudman, 2001; Thomas et al., 2005; Thorp and Lynch, 2000; Vranjic et al., 2000; Weiss et al., 1998). Collectively the two sub-species of *C. monilifera* (subsp. *monilifera* and subsp. *rotundata*) threaten about 200 indigenous species in Australia (Department of Environment Conservation, 2006), including significant rare species such as *Pterostylis truncata* in Victoria. This highly invasive woody shrub drops allelochemical laden litter throughout the year although the quantity varies with season and geographical location (Lindsay and French, 2005; Melland, 2009). Litter and soil properties in boneseed infested areas inhibit germination and growth of native species (McAlpine et al., 2009). We have recently described the significant allelopathic impacts of boneseed on model species and associated native species (Harun et al., 2014).

The current study aimed to investigate the role of temperature in the decomposition of water soluble phenolics (WSP), carbon and nutrients in boneseed litter-mediated soil in relation to phytotoxicity dynamics.

1. Materials and methods

1.1. Sample collection and processing, and seed collection

The You Yangs Regional Park, Victoria (37° 59′ 44″ S, 144° 24′ 39″ E) was selected as the study area as it is representative of

vegetation invaded by boneseed (Roberts, 2008). In September 2012 boneseed litter (above ground) and soil samples were collected from infested areas and soil samples were collected from adjacent areas unoccupied by boneseed. All samples were sealed in plastic bags and immediately transported to the laboratory. Litter samples were air dried at room temperature and extraneous materials were removed prior to being chopped into approximately 1 cm pieces and preserved in sealed plastic bags until the experiments were conducted. Soil samples were air-dried at room temperature until constant weight was achieved and then passed through a 1 mm mesh sieve to remove potential leaf litter contamination and stored in sealed plastic containers until use. Seeds of *Lactuca sativa* (lettuce) were purchased from a local garden supply store, Bunnings, Melbourne, Australia.

1.2. Litter decomposition experimental design

Treatments consisted of three factors including decomposition materials, decomposition periods and exposed temperatures. Decomposition materials comprised a) litter alone, b) litter with soil, and c) soil alone. Three distinct temperatures were investigated in this experiment, 5–15, 15–25 and 25–35°C (night/day). These temperature ranges simulate the natural temperature of various seasons of Australia and New Zealand where boneseed are identified as invasive weed (Bureau of Meteorology, 2014; Meteorological Service of New Zealand Limited, 2014). A twelve hour constant photoperiod was used throughout to exclude the impact of light on decomposition. The study was conducted in 3 individual incubators (Model RI250SG, Thermoline Scientific, Wetherill Park, New South Wales, Australia). For litter alone treatment, 10 mL distilled water (dH_2O) was mixed with 1 g litter in a plastic pot. Litter with soil treatment consisted of 50 g soil, 1 g litter and 40 mL dH_2O while soil alone treatment contained 50 g soil and 35 mL dH_2O. The reason for using varied quantity of water for different treatments was to keep the mixture optimally saturated. 5 mL of microbial inoculum (10%) prepared using rhizosphere soil of boneseed was added to all treatments to mimic the natural microbial activities in the decomposition process. After adding all the materials, the contents in the pots were mixed thoroughly and placed in incubators. Three replicates were maintained in a completely randomized design for each treatment with a total of 162 pots (6 times ∗ 3 temp ∗ 3 decomposition materials ∗ 3 replicates). Every week dH_2O was added to the pots to compensate for evaporative loss, if needed. After 0, 5, 10, 20, 40 and 60 days, aqueous leachates were collected. Briefly, 50 mL water was added to each treatment and agitated for 1.5 hr on an orbital shaker (Orbital Mixer EOM5, Ratek Instruments Pty. Ltd., Boronia, Victoria, Australia) at room temperature. The leachate was centrifuged at 3000 r/min (Econospin 120010, Sorvall Instruments, Germany) for 20 min, and the supernatant was passed through a 0.22 μm filter before storage at −20°C.

1.3. Physicochemical properties of the leachate

Water soluble phenolic concentration was measured using the Folin–Ciocalteu assay (Singleton and Rossi, 1965) with slight modifications using gallic acid as the standard (Bärlocher and

Graça, 2005). Briefly, 0.5 mL leachate was mixed with dH_2O to 1 mL. 5 mL of "2% Na_2CO_3 in 0.1 mo/L NaOH" was added and mixed. After 5 min, 0.5 mL of Folin–Ciocalteu reagent was added, mixed and incubated at room temperature for 2 hr. Finally, absorbance was measured at 760 nm in a spectrophotometer (Libra S12, manufactured by Biochrom Ltd., Cambridge, England), and WSP concentrations were determined based on a standard curve of gallic acid (50–800 μg/mL). Dissolved organic carbon concentration was measured using a TOC analyser (TOC-V w/ TN, Shimadzu, Tokyo, Japan). In every 20 samples, a standard (100 mg/L) dissolved organic carbon (DOC) sample and a dH_2O sample were included to ensure continuous correct reading by the analyser. Leachates were diluted as necessary for DOC analysis. Soil nutrients (PO_4^{-3}, SO_4^{-2}, NO^{-1}, Cl^{-1} and Br^{-1}) concentrations were measured using an ion chromatograph (Shimadzu Ion Chromatograph, Kyoto, Japan). The ion chromatograph was calibrated using a series of standard solutions (concentration 5–500 mg/L) for all anions (PO_4^{-3}, SO_4^{-2}, NO_3^{-1}, Cl^{-1} and Br^{-1}) analysed. pH and electrical conductivity (EC) of the leachates were measured using pH metre (Pocket digital pH metre, 99559, China, made for Dick-smith electronics, Australia) and EC metre (TPS Digital conductivity metre, 2100, TPS Pty Ltd., Brendale, Queensland, Australia), respectively. Osmotic potential was calculated following the equation proposed by McIntyre (1980).

1.4. Bioassay with the leachate

pH of the leachates were adjusted to 6.5 with 1 mol/L NaOH or HCl solution including the dH_2O that was used for control as pH may influence the phytotoxicity (Inderjit and Bhowmik, 2002; Fu and Viraraghavan, 2002) All seeds were surface sterilized with 1.5% (V/V) sodium hypochlorite for 1 min before washing in dH_2O (Jefferson and Pennacchio, 2003). Twenty five seeds of *L. sativa* (test species) were placed in 90 mm Petri dishes lined with two Advantec (85 mm) filter papers moistened with 5 mL of leachates. Distilled water was used as a control (0%). Three replicates were maintained in a completely randomized sign for each treatment. The Petri dishes were sealed with parafilm and incubated in a growth chamber at 25°C in darkness. The number of germinated seedlings (radicle protrudes by ≥1 mm) in all petri dishes were counted daily until cumulative germination levelled off (7 days). Germination indices including total germination (TG), speed of germination (SpG), speed of accumulated germination (SpAG) and coefficient of the rate of germination (CRG) were calculated along with the biometric parameters comprising hypocotyl and radicle length and weight (Chiapusio et al., 1997; Gupta, 1993; Jefferson and Pennacchio, 2003).

1.5. Data analysis

Statistical analysis was conducted using IBM SPSS 21.0. All data were presented as mean ± standard error (SE). Prior to statistical tests data were transformed as necessary. The individual and interactive impacts of decomposition periods, temperature and decomposition materials on WSP, DOC, nutrients, pH, EC, and on germination parameters of test species were evaluated using three-way ANOVA followed by

post hoc LSD test. Significant differences between the means were determined at a 5% level of probability ($p \leq 0.05$). Linear regression was adopted to express the relationship among different parameters.

2. Results

2.1. Impacts on WSP and DOC content

Water soluble phenolics of all treatments generally increased with increasing temperature (Fig. 1). Temperature had little impact on WSP dynamics of litter with soil treatment while soil alone exhibited more impact and litter alone responded moderately. Initially, litter alone treatment had about two and half times more WSP than the litter with soil treatment, however, at final stage of decomposition (day 60) this difference was about five times. The trend in WSP concentration over time was not linear but it showed a decrease by 38% and 73% in litter alone and litter with soil treatments, respectively, while in soil alone treatment it was increased by 15% compared with initial level. Temperature, decomposition material and decomposition period all exhibited significant individual and interactive effects on the WSP content of the leachates (Table 1).

Likewise, DOC increased with increasing temperature in all treatments. On an average, DOC at 15–25°C and 25–35°C was increased by 8.8% and 16.7% (litter alone), 9.6% and 9.8% (litter with soil), and 22.6% and 60.3% (soil alone) when compared with 5–15°C (Fig. 2). Initially, litter alone treatment had about one and half times more DOC than the litter with soil treatment, however, at final stage of decomposition (day 60) this difference tended to about two times. DOC showed no clear trend in relation to decomposition time with a final reduction of 47% and 54% for litter alone and litter with soil treatment (from days 0 to 60) while in soil alone treatment it was unvaried. Temperatures, decomposition materials and decomposition periods all showed both individual and interactive significant effects on the DOC content of leachates (Table 1). DOC had a very strong correlation ($r = 0.915$) with WSP throughout the decomposition periods and across the temperatures (Fig. 3).

2.2. Dynamics of soil nutrients

NO_3^{-1} decreased with increasing decomposition temperature for all treatments (Fig. 4 and Appendix A Table S1). Litter with soil had more NO_3^{-1} than litter alone treatments but less than the soil alone treatments with the exception at 25–35°C when soil alone contained slightly lower than the litter with soil treatment. NO_3^{-1} generally decreased with decomposition period for all decomposition materials with the exception for litter alone treatment in which NO_3^{-1} disappeared, returned at low concentrations before disappearing again. On final stage of decomposition treatment (day 60), NO_3^{-1} was absent in all treatments. The boxplot showed that NO_3^{-1} variation for all decomposition materials with temperature was more consistent at 5–15°C compared with other temperatures that reflects some extreme outliers. PO_4^{-3} concentration in the litter with soil treatment increased with temperature but decreased in soil alone treatment while litter alone treatment showed no
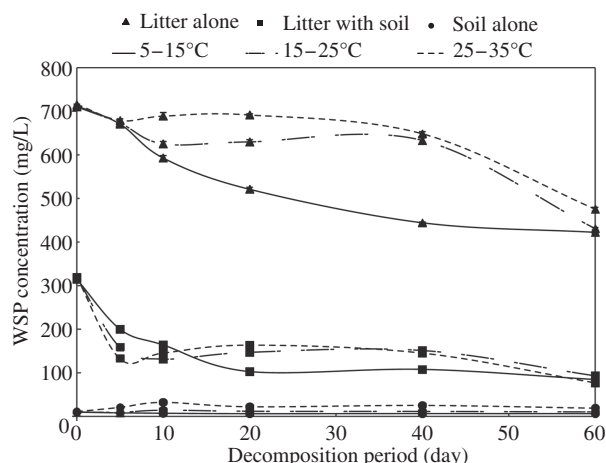
Fig. 1 – Water soluble phenolic (WSP) content of different decomposition materials (litter alone, litter with soil, and soil alone) exposed to various temperatures.

consistent pattern (Fig. 4 and Appendix A Table S2). Leachate of litter with soil treatment contained more PO_4^{-3} compared with litter alone and soil alone treatment respectively at constant temperature. PO_4^{-3} decreased with decomposition period for all treatments with the exception on day 5 for litter alone treatment when it was increased by two fold compared with initial concentration. SO_4^{-2} concentration decreased by 16% and 28% (litter alone), and 34% and 61% (litter with soil) with increasing temperature from 5–15°C to 15–25°C and 25–35°C respectively but in soil alone treatment it was increased by 10% and 3% respectively (Fig. 4 and Appendix A Table S3). Litter alone contained the highest SO_4^{-2} concentration followed by litter with soil and soil alone at the same treatment condition. SO_4^{-2} concentration decreased with decomposition time for all decomposition materials, and ultimately disappeared in litter with soil and soil alone treatment. Cl^{-1} concentrations in all treatments was almost unvaried with temperature except for the litter alone that slightly decreased with temperature (Fig. 4 and Appendix A Table S4). Cl^{-1} concentration had exhibited little variation with decomposition time with the exception on day 5 when it decreased rapidly compared with initial concentration (day 0). No bromide was found in soil alone treatment, although very little (1.1–1.7 mg/L) Br^{-1} existed in other treatments with no clear pattern of change with temperature and decomposition period (Fig. 4 and Appendix A Table S5).

2.3. Changing aspects of pH, EC and osmotic potential

On average pH decreased with increasing temperature in litter alone treatment but increased in soil alone treatment while it remained unchanged in litter with soil treatment during the decomposition periods (Fig. 5). At low and medium temperatures (5–15 and 15–25°C) pH of litter with soil treatment was lower (9% and 6%) than the litter alone treatment but similar to the soil alone treatment while at high temperature (25–35°C) it was 4% higher and 6% lower than the litter alone treatment and soil alone treatment respectively. Although a final increase of pH
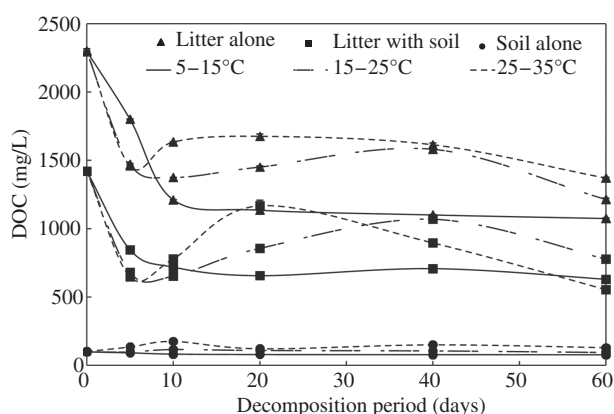
Table 1 – ANOVA output (F — ratios) displaying the effects of decomposed materials (M), decomposition period (P) and temperature (T) on dissolved organic carbon (DOC), water soluble phenolics (WSP), total germination (TG), speed of germination (SpG), speed of accumulated germination (SpAG), coefficient of rate of germination (CRG), hypocotyl and radical length (HL and RL) and weight (HW and RW).

Parameters	M	P	T	M × P	M × T	P × T	M × P × T
DOC	$F_{2,\,108} = 201792^{***}$	$F_{5,\,108} = 3878^{***}$	$F_{2,\,108} = 1302^{***}$	$F_{10,\,108} = 1199^{***}$	$F_{4,\,108} = 103^{***}$	$F_{10,\,108} = 436^{***}$	$F_{20,\,108} = 130^{***}$
WSP	$F_{2,\,108} = 235165^{***}$	$F_{5,\,108} = 1760^{***}$	$F_{2,\,108} = 1339^{***}$	$F_{10,\,108} = 752^{***}$	$F_{4,\,108} = 497^{***}$	$F_{10,\,108} = 169^{***}$	$F_{20,\,108} = 48^{***}$
TG	$F_{2,\,108} = 88^{***}$	$F_{5,\,108} = 20^{***}$	$F_{2,\,108} = 15^{***}$	$F_{10,\,108} = 15^{***}$	$F_{4,\,108} = 1.2$	$F_{10,\,108} = 2$	$F_{20,\,108} = 0.64$
SpG	$F_{2,\,108} = 2864^{***}$	$F_{5,\,108} = 93^{***}$	$F_{2,\,108} = 277^{***}$	$F_{10,\,108} = 26^{***}$	$F_{4,\,108} = 45^{***}$	$F_{10,\,108} = 37^{***}$	$F_{20,\,108} = 25^{***}$
SpAG	$F_{2,\,108} = 2552^{***}$	$F_{5,\,108} = 97^{***}$	$F_{2,\,108} = 274^{***}$	$F_{10,\,108} = 27^{***}$	$F_{4,\,108} = 45^{***}$	$F_{10,\,108} = 40^{***}$	$F_{20,\,108} = 21^{***}$
CRG	$F_{2,\,108} = 2616^{***}$	$F_{5,\,108} = 100^{***}$	$F_{2,\,108} = 301^{***}$	$F_{10,\,108} = 24^{***}$	$F_{4,\,108} = 76^{***}$	$F_{10,\,108} = 53^{***}$	$F_{20,\,108} = 27^{***}$
HL	$F_{2,\,108} = 3320^{***}$	$F_{5,\,108} = 136^{***}$	$F_{2,\,108} = 1422^{***}$	$F_{10,\,108} = 303^{***}$	$F_{4,\,108} = 273^{***}$	$F_{10,\,108} = 163^{***}$	$F_{20,\,108} = 123^{***}$
HW	$F_{2,\,108} = 3447^{***}$	$F_{5,\,108} = 195^{***}$	$F_{2,\,108} = 1348^{***}$	$F_{10,\,108} = 348^{***}$	$F_{4,\,108} = 267^{***}$	$F_{10,\,108} = 187^{***}$	$F_{20,\,108} = 97^{***}$
RL	$F_{2,\,108} = 17790^{***}$	$F_{5,\,108} = 722^{***}$	$F_{2,\,108} = 1612^{***}$	$F_{10,\,108} = 272^{***}$	$F_{4,\,108} = 1298^{***}$	$F_{10,\,108} = 317^{***}$	$F_{20,\,108} = 333^{***}$
RW	$F_{2,\,108} = 9881^{***}$	$F_{5,\,108} = 177^{***}$	$F_{2,\,108} = 1046^{***}$	$F_{10,\,108} = 301^{***}$	$F_{4,\,108} = 540^{***}$	$F_{10,\,108} = 188^{***}$	$F_{20,\,108} = 180^{***}$

*** Strongly significant ($p < 0.001$), ** significant ($p = 0.001$ to <0.01), * poorly significant ($p = 0.01$ to ≤ 0.05), and blank means non-significant.

(from day 0 to day 60) was generally identified, however, day to day trend of pH dynamics among the temperatures, decomposition periods and decomposition materials were not consistent. The smaller box (interquartile range) of pH data for 15–25°C exhibited less variation of pH compared with 5–15°C and 25–35°C respectively (Fig. 5).
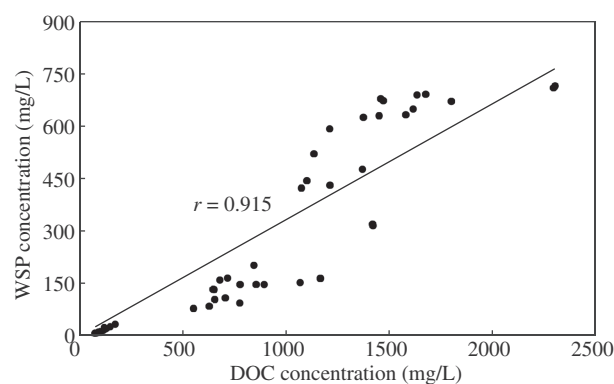
EC of litter alone and litter with soil increased with increasing temperature while in soil alone treatment it decreased (Fig. 5). EC of litter with soil treatment was 75%–83% higher than soil alone treatment while it was 6%–18% lower than litter alone treatment at low and medium temperature but slightly higher at high temperature (Fig. 5). The trend in EC dynamics with decomposition period was not consistent, though, a final (day 0 to 60) decrease of EC was identified for all treatments. The box plot showed smaller variation in EC for temperature 5–15°C than that of higher temperatures, and no extreme EC was found as all data fall within the upper and lower fences. Osmotic potential exhibited a similar pattern to that observed for EC (Fig. 5). All the interactive and individual impacts of decomposition period, materials and temperature on pH, EC and osmotic potential were found to be strongly significant ($p < 0.001$) (Appendix Table S6–S8).

2.4. Phytotoxicity dynamics of leachates

Decomposition temperature, period and materials all had individual significant impacts on TG of *L. sativa* exposed to leachates, although the interactive effects for most cases were not significant (Table 1). Generally, TG increased with initial increase in decomposition temperature (5–15°C to 15–25°C) but decreased with further increase to 25–35°C. Leachate from litter with soil had less impact on TG compared with litter alone but more impact on TG compared with soil alone treatments. TG varied inconsistently with time with a final increase of 16% and 4% (from day 0 to 60) for litter alone and litter with soil treatments, respectively, while it was unchanged for soil alone treatment. A strong inhibition (11%–20%) on TG was observed in the litter alone treatment at the initial level while all moderate impacts (5%–10%) were confined to 25–35°C of litter alone treatment (Fig. 6). SpG, SpAG and CRG were strongly significantly affected by all the experimental parameters (Table 1). Speed of germination was generally decreased with increasing decomposition temperature (Fig. 7). *L. sativa* exposed to leachate of litter with soil had a greater SpG (25%) than that of litter alone treatment and less SpG (47%) compared with soil alone treatment. SpG increased (from day 0 to 60) by

Fig. 2 – Dissolved organic carbon (DOC) concentration of different decomposition materials exposed to various temperatures.

Fig. 3 – Correlation between dissolved organic carbon (DOC) and water soluble phenolic (WSP) content of leachate (all decomposed materials across the temperatures and decomposition periods).
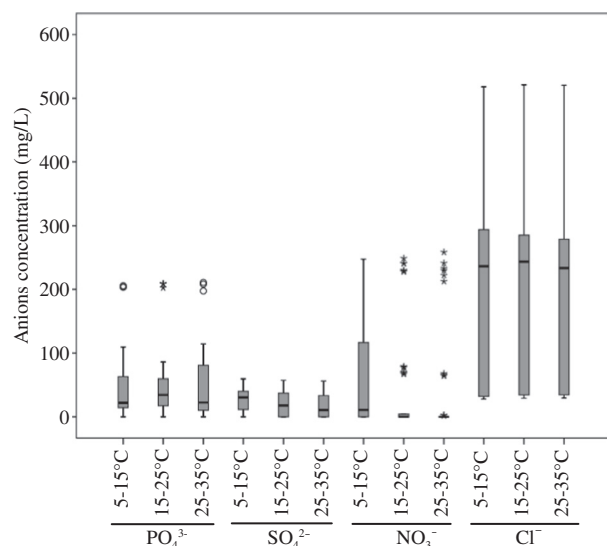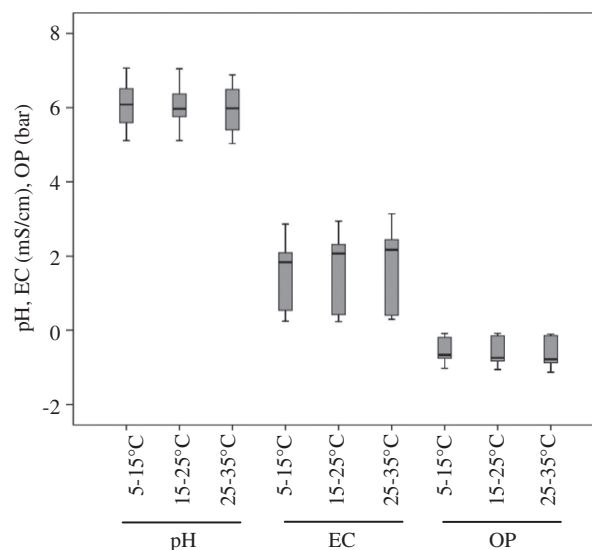
Fig. 4 – Nutrient dynamics of different decomposition materials with varied temperature (across the decomposition period).

Fig. 5 – pH, electrical conductivity (EC) and osmotic potential (OP) dynamics of different decomposition materials with varied temperature (across the decomposition period).

52%, 26% and 0% for litter alone, litter with soil and soil alone treatment, respectively. SpAG and CRG exhibited a similar pattern to that observed for SpG (data not shown).

Hypocotyl length of *L. sativa* decreased by 39% and 63% (litter alone), 24% and 42% (litter with soil) and 5% and 7% (soil alone) with increasing decomposition temperature from 5–15°C to 15–25°C and 25–35°C (Fig. 8). *L. sativa* exposed to litter with soil leachate had longer (33%) hypocotyl length compared with litter alone treatment but smaller (37%) than the soil alone treatment. Hypocotyl length increased (from day 0 to 60) by 276% and 5% for litter alone and litter with soil treatment but it was decreased by 16% for soil alone treatment. Radical length of *L. sativa* decreased by 49% and 82% (litter alone), and 40% and 67% (litter with soil) with increasing decomposition temperature from 5–15°C to 15–25°C and 25–35°C while for soil alone treatment it was increased by 17% and 24% (Fig. 8). *L. sativa* exposed to litter with soil leachate had longer (19%) radical length compared with litter alone treatment but smaller (270%) than the soil alone treatment. Radical length increased (from day 0 to 60) by 971%, 30% and 50% for litter alone, litter with soil and soil alone treatments, respectively. Temperature, decomposition period and decomposition materials significantly affected (both individually and interactively) the hypocotyl and radical length and weight (Table 1). SpG and radical length showed correlation with WSP content of leachate, most significantly between WSP and SpG ($r = 0.817$, and 0.646) (Fig. 9).

3. Discussion

This study revealed varied impacts of temperature, decomposition time and decomposition material on WSP, DOC, nutrient content, pH and phytotoxicity dynamics from boneseed litter. The substantial differential of the rate of WSP decomposition in litter alone and litter with soil treatment may be due to the use of phenolics as the source of carbon by soil microorganisms (Souto et al., 2000), in addition to the influence of soil nutrients (Rice, 1979). We found increasing WSP with increasing temperature but a decrease in WSP with time regardless of temperature. Janas et al. (2000) in results similar to ours, found that the concentration and stability of phenolic compounds in soil ecosystems varied with decomposition period and temperature. Similarly, the findings of Spigno et al. (2007) showed that high temperature leads to an increase in phenolic content in litter occupied soil while May and Ash (1990a) described a decrease in phenolics over time.
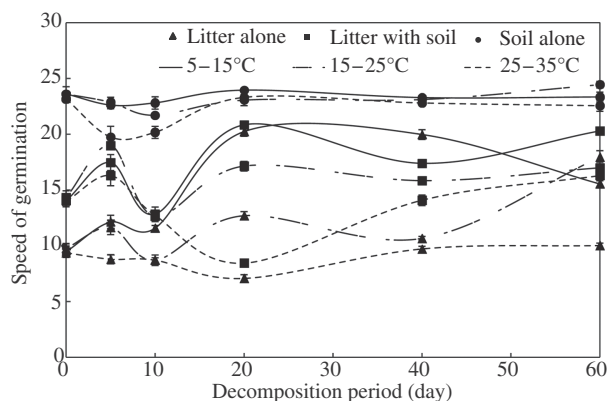
The effect of temperature on DOC dynamics observed in the current study supports the Thornley and Cannell (2001) hypothesis that DOC increases with increasing temperature. Although temperature may be a major driver of increased DOC, rainfall, soil quality and microorganisms may be additional factors in soil carbon dynamics (Beare et al., 1992; Hobbie, 1992, 1996; Salamanca et al., 2003; Van Vuuren et al., 1992). The large (two fold) decrease in DOC in litter added soil treatment over time (initial to final) may be due to microbial decomposition as suggested by Parker et al. (1984). The increasing carbon in litter-mediated soil at high temperature may represent a positive feedback to global warming if released to the atmosphere, as suggested by Mack et al. (2004). We found low NO_3^{-1} but high DOC with increasing temperature which may indicate increasing denitrification with increasing DOC. A similar result by Dodla et al. (2008) suggested that DOC positively influences denitrification. This study suggested a reduction of NO_3^{-1} with temperature with a simultaneous increase in DOC with temperature causing a high C/N ratio (*e.g.*, in litter with soil treatment). Additionally, WSP increased with temperature suggesting the high C/N ratio underpinned increasing allelochemical concentration which aligns well with a previously formulated C/N balance hypothesis (Bryant et al., 1983).

In our study, litter added PO_4^{-3}, SO_4^{-2}, Cl^{-1} and Br^{-1} content to the soil, confirming an earlier study (Jose et al., 2000), although NO_3^{-1} content was severely depleted with addition of litter. The degradation of soil NO_3^{-1} may be due to the denitrification or suppression of nitrogen fixing bacteria by allelopathins (Northup et al., 1998). We found depletion of NO_3^{-1} with temperature but

■ 11%–20% inhibition   ■ 5%–10% inhibition   ■ <5% inhibition   □ No inhibition
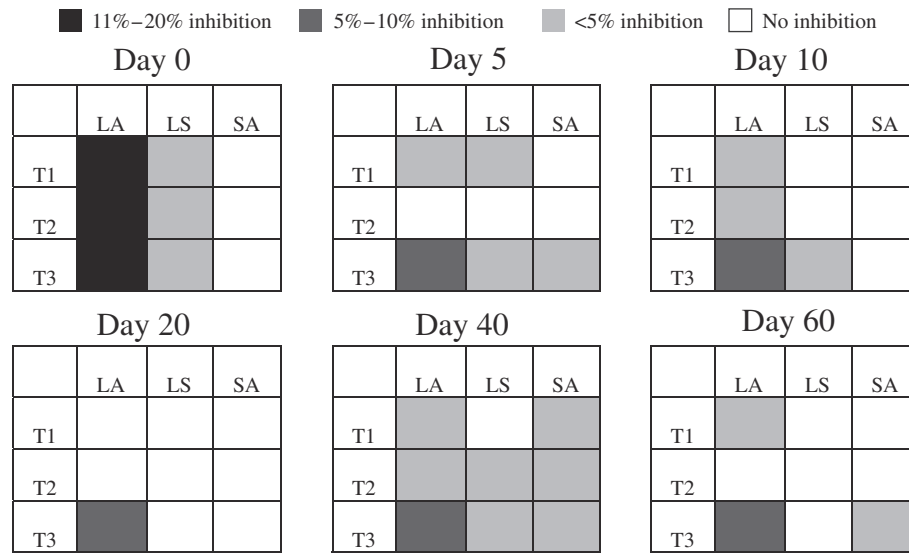
Fig. 6 – Total germination (TG) inhibition matrix of *L. sativa* by leachate of different decomposed materials (litter alone (LA), litter with soil (LS), and soil alone (SA)) exposed to various temperatures (5–15 °C (T1), 15–25 °C (T2) and 25–35 °C (T3)).

other nutrients showed no obvious trend with temperature that support the findings of an earlier study (Cheng et al., 2014). The germination parameters of test species increased with decomposition time while soil nutrient was decreased. The reduction of WSP at same pattern of nutrient might be the reason which might limit the germination previously. In our study it is clear that the role of WSP overweighed the role of nutrient, however, in contrast, Inderjit and Dakshini (1994) addressed that nutrient released from the decomposed plant litter may play an important role in overcoming allelopathic effects, depending on the litter types and microenvironment and microbial activities. Litter quality influences decomposition of carbon that in turn controls nitrogen mineralization rates in soil (Hobbie, 1992). Our results suggest substantial impact of temperature on nutrient content of the soil in association with litter addition. Weed invasion may alter established patterns of nutrient cycling (Standish et al., 2004) that may lead to a decrease in ecosystem stability (McIvor, 2001) and biodiversity (Wedin and Tilman, 1990).

Litter alone treatment showed a decreasing trend of pH with increasing temperature, though pH increased with increasing temperature in both litter with soil and soil alone treatments. At any specific temperature, litter with soil had a higher pH than the soil alone treatment indicating that litter decomposition plays an important role in altering soil pH. These results reveal

Fig. 7 – Speed of germination (SpG) of *L. sativa* exposed to leachate of different decomposed materials at various temperatures.
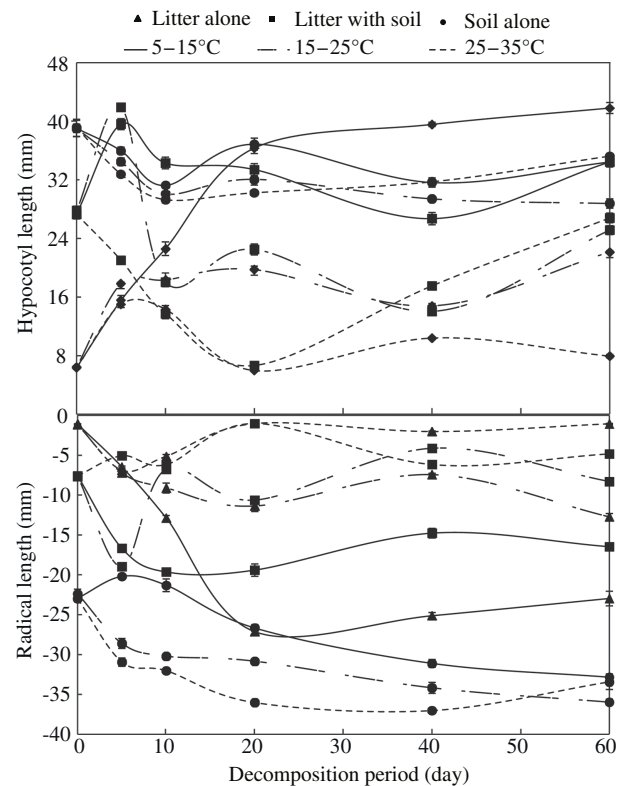
Fig. 8 – Hypocotyl and radical length of *L. sativa* exposed to leachate of different decomposed materials at various temperatures.
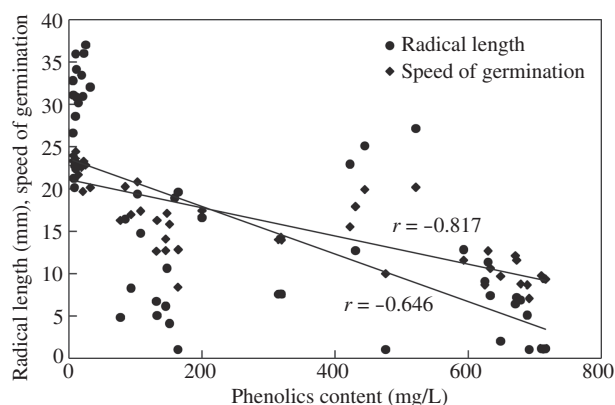
Fig. 9 – Correlation between phenolics content of leachate (all decomposed materials across the temperatures and decomposition periods) and speed of germination ($r = -0.817$), and between phenolics contents and radical length ($r = -0.646$) of _L. sativa_.

that not only temperature but also contact of soil with litter, in conjunction with soil microbial activities, nutrient and soil organic carbon, influence the pH of soil. pH may affect the nutrient content of soil (Dewes, 1996) and thereby, plant growth may be affected. Our results exhibited a similar trend to that reported by Dewes (1996) of decreasing soil nitrogen with increasing temperature and pH. An explanation of the low NO_3^{-1} in litter with soil treatment observed in this study might be explained by denitrification processes as the pH level we observed are within the range deemed suitable for denitrification (Stevens et al., 1998). Bremner and Shaw (1958) described an increase in denitrification with increasing pH and temperature. We found that the osmotic potential of litter when combined with soil increased with increasing temperature and variably increased with decomposition period but may not substantially contribute to phytotoxicity as reported by Anderson and Loucks (1966). The findings of this study regarding the relation between soil carbon and nutrient (nitrate and phosphate) i.e., increasing carbon with decreasing NO_3^{-1} and increasing PO_4^{-3} support the previous study (Ouyang et al., 2008).

SpG decreased with increasing decomposition temperature which is likely due to WSP concentration. SpG was significantly lower in litter with soil treatment as compared with soil alone treatment (across the temperatures and decomposition periods) which may be attributed to the WSP content of the treatments. Over time, as WSP concentrations decreased, SpG increased. Inhibition of SpG with increasing aqueous extract of boneseed was identified in an earlier study (Harun et al., 2014). Speed of germination has been generally considered as the key indicator among germination indices in allelopathic studies while TG reflects allelopathic impact poorly (Chiapusio et al., 1997). The very strong negative correlations between the WSP content of the leachates and SpG of test plants suggest that the WSP may be responsible for this phytotoxic effect on the test plant.

The inhibition of hypocotyl and radical length and weight of _L. sativa_ in our study is aligned with Steinsiek et al. (1982) suggesting that phytotoxicity had a proportional relationship with increasing temperature. Additional inhibitory effects to

biometric parameters of test species exposed to leachate of litter with soil treatment compared with soil alone treatment also supports the phytotoxicity of boneseed litter. Suppression of associated species by allelopathic plants indicates influences by several factors including litter distribution that may vary with season (del Moral and Muller, 1970). Litter and soil properties in the boneseed infested areas have been shown to inhibit germination and growth of native species (McAlpine et al., 2009). Our study revealed more obvious phytotoxic effects on the radical compared with hypocotyl, a finding which is similar to other allelopathic studies (Kobayashi et al., 2008). The strong correlation between WSP contents of decomposed leachates and radical length of _L. sativa_ may indicate the involvement of leachate WSP in phytotoxicity. However, nutrient immobilization, depletion of O_2 in the soil, toxicity of CO_2 produced in soil may also be involved in the phytotoxicity of litter on neighbouring species (de Jong and Klinkhamer, 1985; Rice, 1979).

Similar to our findings of the inverse relation of boneseed litter phytotoxicity with time (Figs. 7 and 8), Bonanomi et al. (2011) suggested changing phytotoxicity of _Medicago sativa_ litter that was linked to an association with soil microorganisms over time. Likewise, other studies also suggested higher levels of impact on test species during the early stages of litter decomposition followed by decreases in phytotoxicity over time (Hussain, 1980; Jäderlund et al., 1996; Lodhi, 1978), though this varied with plant species (Bonanomi et al., 2005). The role of soil microorganisms in natural regeneration failure of plant species may be as important a factor as phenolics and these phenolics may also inhibit the growth and activities of soil beneficial microorganisms (Souto et al., 2000). The ability of exotic species to change soil-based ecosystems may enable them to invade and outcompete native species (Fogarty and Facelli, 1999). Although our findings indicate phytotoxicity of boneseed litter, field evidence is imperative to demonstrate allelopathic impact in a more authentic way as edaphic and environmental factors work together in influencing allelopathic effects (Inderjit and Duke, 2003).

4. Conclusions

Both WSP and DOC increased with temperature showing a strong correlation between them. We found strong negative impact of increasing temperature on soil NO_3^{-1} content. Phytotoxicity of boneseed litter-mediated soil increased with temperature. A substantial reduction of phytotoxic effect was observed after 2 month decomposition of boneseed litter correlating with the decreasing WSP content. A strong correlation between radical length and the WSP content of the leachates may suggest phytotoxicity by litter WSP. This study clarified the complex interactivity among temperature, carbon, nutrients and WSP dynamics of litter occupied soil environments that work together to influence phytotoxicity. We conclude that regeneration of locally native species may be confined to or differentially impacted depending on the natural season of germination of the individual species concerned. Large scale litter decomposition studies in forest ecosystems relating WSP, nutrient and carbon dynamics may link closely with phytotoxicity and biodiversity and ultimately, all may relate to temperature and climate change.

Acknowledgment

Appendix A. Supplementary data

Supplementary data associated with this article can be found in online version at http://dx.doi.org/10.1016/j.jes.2014.12.017.

REFERENCES

An, M., Pratley, J., Haig, T., 2001. Phytotoxicity of *Vulpia* residues: III. Biological activity of identified allelochemicals from *Vulpia myuros*. J. Chem. Ecol. 27 (2), 383–394.

An, M., Johnson, I.R., Lovett, J.V., 2002. Mathematical modelling of residue allelopathy: the effects of intrinsic and extrinsic factors. Plant Soil 246 (1), 11–22.

Anderson, R.C., Loucks, O.L., 1966. Osmotic pressure influence in germination tests for antibiosis. Science 152 (3723), 771–773.

Baldwin, I.T., Olson, R.K., Reiners, W.A., 1983. Protein binding phenolics and the inhibition of nitrification in subalpine balsam fir soils. Soil Biol. Biochem. 15 (4), 419–423.

Bärlocher, F., Graça, M., 2005. Total phenolics. In: Graça, M., Bärlocher, F., Gessner, M. (Eds.), Methods to Study Litter Decomposition. Springer, Netherlands, pp. 97–100.

Beare, M.H., Parmelee, R.W., Hendrix, P.F., Cheng, W., Coleman, D.C., Crossley Jr., D., 1992. Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecol. Monogr. 62 (4), 569–591.

Bonanomi, G., Sicurezza, M.G., Caporaso, S., Esposito, A., Mazzoleni, S., 2005. Phytotoxicity dynamics of decaying plant materials. New Phytol. 169 (3), 571–578.

Bonanomi, G., Antignani, V., Barile, E., Lanzotti, V., Scala, F., 2011. Decomposition of *Medicago sativa* residues affects phytotoxicity, fungal growth and soil-borne pathogen diseases. J. Plant Pathol. 93 (1), 57–69.

Bremner, J., Shaw, K., 1958. Denitrification in soil. II. Factors affecting denitrification. J. Agric. Sci. 51 (1), 40–52.

Bryant, J.P., Chapin III, F.S., Klein, D.R., 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40 (3), 357–368.

Bureau of Meteorology, 2014. Government of Australia, Australia.

Cheng, Y., Wang, J., Wang, S.Q., Cai, Z.C., Wang, L., 2014. Effects of temperature change and tree species composition on N_2O and NO emissions in acidic forest soils of subtropical China. J. Environ. Sci. 26 (3), 617–625.

Chiapusio, G., Sánchez, A., Reigosa, M., González, L., Pellissier, F., 1997. Do germination indices adequately reflect allelochemical effects on the germination process? J. Chem. Ecol. 23 (11), 2445–2453.

Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., et al., 2001. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biol. 7 (4), 357–373.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440 (7081), 165–173.

Davies, R.J., 1988. Sheet mulching as an aid to broadleaved tree establishment II. Comparison of various sizes of black polythene mulch and herbicide treated spot. Forestry 61 (2), 107–124.

de Jong, T.J., Klinkhamer, P.G.L., 1985. The negative effects of litter of parent plants of *Cirsium vulgare* on their offspring: autotoxicity or immobilization? Oecologia 65 (2), 153–160.

del Moral, R., Muller, C.H., 1970. The allelopathic effects of *Eucalyptus camaldulensis*. Am. Midl. Nat. 83 (1), 254–282.

Department of Environment Conservation, 2006. NSW Threat Abatement Plan: Invasion of Native Plant Communities by *Chrysanthemoides monilifera* (Bitou Bush and Boneseed). Department of Environment and Conservation, (New South Wales) Hurstville, Australia.

Dewes, T., 1996. Effect of pH, temperature, amount of litter and storage density on ammonia emissions from stable manure. J. Agric. Sci. 127 (4), 501–509.

Dodla, S.K., Wang, J.J., DeLaune, R.D., Cook, R.L., 2008. Denitrification potential and its relation to organic carbon quality in three coastal wetland soils. Sci. Total Environ. 407 (1), 471–480.

Ens, E.J., French, K., Bremner, J.B., 2009. Evidence for allelopathy as a mechanism of community composition change by an invasive exotic shrub, *Chrysanthemoides monilifera* spp. rotundata. Plant Soil 316 (1), 125–137.

Facelli, J.M., Pickett, S.T., 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57 (1), 1–32.

Flanagan, P., Cleve, K.V., 1983. Nutrient cycling in relation to decomposition and organic-matter quality in taiga ecosystems. Can. J. Forest Res. 13 (5), 795–817.

Fogarty, G., Facelli, J.M., 1999. Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. Plant Ecol. 144 (1), 27–35.

Foster, B.L., Gross, K.L., 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. Ecology 79 (8), 2593–2602.

Fu, Y.Z., Viraraghavan, T., 2002. Removal of Congo Red from an aqueous solution by fungus *Aspergillus niger*. Adv. Environ. Res. 7 (1), 239–247.

Gosz, J., 1981. Nitrogen cycling in coniferous ecosystems. Ecol. Bull. 33, 405–426.

Groves, R.H., 2008. Keynote address: research on bitou bush and boneseed—a work in progress. Plant Prot. Q. 23 (1), 15–19.

Gupta, P., 1993. Seed vigour testing. In: Agarwal, P.K. (Ed.), Handbook of Seed Testing. National Seed Corporation, New Delhi, pp. 242–249.

Halligan, J.P., 1975. Toxic terpenes from *Artemisia californica*. Ecology 56 (4), 999–1003.

Harun, M.A.Y.A., Robinson, R.W., Johnson, J., Uddin, M.N., 2014. Allelopathic potential of *Chrysanthemoides monilifera* subsp. *monilifera* (boneseed): a novel weapon in the invasion processes. S. Afr. J. Bot. 93, 157–166.

Hobbie, S.E., 1992. Effects of plant species on nutrient cycling. Trends Ecol. Evol. 7 (10), 336–339.

Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol. Monogr. 66 (4), 503–522.

Holland, E.A., Coleman, D.C., 1987. Litter placement effects on microbial and organic matter dynamics in an agroecosystem. Ecology 68 (2), 425–433.

Horner, J.D., Gosz, J.R., Cates, R.G., 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. Am. Nat. 132 (6), 869–883.

Hussain, F., 1980. Allelopathic effects of Pakistani weeds: *Euphorbia granulata* Forssk. Oecologia 45 (2), 267–269.

Inderjit, 1996. Plant phenolics in allelopathy. Bot. Rev. 62 (2), 186–202.

Inderjit, Dakshini, K.M.M., 1994. Allelopathic effect of *Pluchea ianceolata* (Asteraceae) on characteristics of four soils and tomato and mustard growth. Am. J. Bot. 81 (7), 799–804.

Inderjit, del Moral, R., 1997. Is separating resource competition from allelopathy realistic? Bot. Rev. 63 (3), 221–230.

Inderjit, Bhowmik, P.C., 2002. Allelochemicals phytotoxicity in explaining weed invasiveness and their function as herbicide analogues. In: Mallik, A.U. (Ed.), Chemical Ecology of Plants: Allelopathy in Aquatic and Terrestrial Ecosystems. Birkhäuser-Verlag, pp. 187–197.

Inderjit, Duke, S.O., 2003. Ecophysiological aspects of allelopathy. Planta 217 (4), 529–539.

Inderjit, Mallik, A.U., 1997. Effect of phenolic compounds on selected soil properties. Forest Ecol. Manag. 92 (1-3), 11–18.

Jäderlund, A., Zackrisson, O., Nilsson, M.-C., 1996. Effects of bilberry (Vaccinium myrtillus L.) litter on seed germination and early seedling growth of four boreal tree species. J. Chem. Ecol. 22 (5), 973–986.

Janas, K.M., Cvikrová, M., Pałagiewicz, A., Eder, J., 2000. Alterations in phenylpropanoid content in soybean roots during low temperature acclimation. Plant Physiol. Biochem. 38 (7-8), 587–593.

Jefferson, L.V., Pennacchio, M., 2003. Allelopathic effects of foliage extracts from four Chenopodiaceae species on seed germination. J. Arid Environ. 55 (2), 275–285.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78 (7), 1946–1957.

Jose, S., Gillespie, A.R., Seifert, J.R., Mengel, D.B., Pope, P.E., 2000. Defining competition vectors in a temperate alley cropping system in the midwestern USA: 3. Competition for nitrogen and litter decomposition dynamics. Agrofor. Syst. 48 (1), 61–77.

Kobayashi, K., 2004. Factors affecting phytotoxic activity of allelochemicals in soil. Weed Biol. Manag. 4 (1), 1–7.

Kobayashi, K., Itaya, D., Mahatamnuchoke, P., Pornprom, T., 2008. Allelopathic potential of itchgrass (Rottboellia exaltata L. f.) powder incorporated into soil. Weed Biol. Manag. 8 (1), 64–68.

Kumar, V., Brainard, D.C., Bellinder, R.R., 2009. Suppression of Powell amaranth (Amaranthus powellii) by buckwheat residues: role of allelopathy. Weed Sci. 57 (1), 66–73.

Lindsay, E.A., French, K., 2005. Litterfall and nitrogen cycling following invasion by Chrysanthemoides monilifera ssp. rotundata in coastal Australia. J. Appl. Ecol. 42 (3), 556–566.

Liu, Y., Li, F., Huang, Q.X., 2013. Allelopathic effects of gallic acid from Aegiceras corniculatum on Cyclotella caspia. J. Environ. Sci. 25 (4), 776–784.

Lodhi, M.A.K., 1978. Allelopathic effects of decaying litter of dominant trees and their associated soil in a lowland forest community. Am. J. Bot. 65 (3), 340–344.

Mack, M.C., Schuur, E.A., Bret-Harte, M.S., Shaver, G.R., Chapin, F.S., 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431 (7007), 440–443.

May, F.E., Ash, J.E., 1990a. An assessment of the allelopathic potential of Eucalyptus. Aust. J. Bot. 38 (3), 245–254.

May, F.E., Ash, J.E., 1990b. An assessment of the allelopathic potential of eucalyptus. Aust. J. Bot. 38 (3), 245–254.

McAlpine, K.G., Timmins, S.M., Westbrooke, I., 2009. Boneseed (Chrysanthemoides monilifera ssp. monilifera) invasion effects on native regeneration in New Zealand coastal plant communities. N. Z. J. Ecol. 33 (1), 72–82.

McGinnies, W.J., 1987. Effects of hay and straw mulches on the establishment of seeded grasses and legumes on rangeland and a coal strip mine. J. Range Manag. 40 (2), 119–121.

McIntyre, D., 1980. Basic relationships for salinity evaluation from measurements on soil solution. Aust. J. Soil Res. 18 (2), 199–206.

McIvor, J.G., 2001. Litterfall from trees in semiarid woodlands of north-east Queensland. Aust. Ecol. 26 (2), 150–155.

Melland, R.L., 2009. Management of Boneseed (Chrysanthemoides monilifera ssp. monilifera)(L.) T. Norl. Using Fire, Herbicides and Other Techniques in Australian Woodlands. (PhD Thesis). University of Adelaide.

Meteorological Service of New Zealand Limited, 2014. Government of New Zealand, New Zealand.

Mitchell, J.D., Lockaby, B.G., Brantley, E.F., 2011. Influence of Chinese privet (Ligustrum sinense) on decomposition and nutrient availability in Riparian forests. Invasive Plant Sci. Manag. 4 (4), 437–447.

Northup, R.R., Dahlgren, R.A., McColl, J.G., 1998. Polyphenols as regulators of plant–litter–soil interactions in northern California's pygmy forest: a positive feedback? Biogeochemistry 42 (1-2), 189–220.

Ouyang, X.J., Zhou, G.Y., Huang, Z.L., Zhou, C.Y., Li, J., Shi, J.H., et al., 2008. Effect of N and P addition on soil organic C potential mineralization in forest soils in South China. J. Environ. Sci. 20 (9), 1082–1089.

Parker, L.W., Santos, P.F., Phillips, J., Whitford, W.G., 1984. Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual, Lepidium lasiocarpum. Ecol. Monogr. 54 (3), 339–360.

Parsons, W.T., 1973. Noxious Weeds of Victoria. Inkata Press Proprietary Ltd., Australia.

Rice, E.L., 1965. Inhibition of nitrogen-fixing and nitrifying bacteria by seed plants IV. The inhibitors produced by Ambrosia elatior and A. psilostachya. SW Nat. 10 (4), 248–255.

Rice, E.L., 1979. Allelopathy—an update. Bot. Rev. 45 (1), 15–109.

Rice, E.L., 1984. Allelopathy. Academic Press, Florida.

Roberts, D., 2008. A history of boneseed control in the You Yangs Regional Park, Victoria. Plant Prot. Q. 23 (1), 51.

Rudman, T., 2001. Tasmanian Weed Status Report: Boneseed (Chrysanthemoides monilifera subsp monilifera). Nature Conservation Branch, Department of Primary Industries, Water and Environment, Australia.

Salamanca, E.F., Kaneko, N., Katagiri, S., 2003. Rainfall manipulation effects on litter decomposition and the microbial biomass of the forest floor. Appl. Soil Ecol. 22 (3), 271–281.

Saura-Mas, S., Estiarte, M., Peñuelas, J., Lloret, F., 2012. Effects of climate change on leaf litter decomposition across post-fire plant regenerative groups. Environ. Exp. Bot. 77, 274–282.

Schlesinger, W.H., Andrews, J.A., 2000. Soil respiration and the global carbon cycle. Biogeochemistry 48 (1), 7–20.

Shaver, G., Chapin III, F., 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, USA. Arct. Alp. Res. 18 (3), 261–268.

Singleton, V.L., Rossi Jr., J.A., 1965. Colorimetry of total phenolics with phosphomolybdic–phosphotungstic acid reagents. Am. J. Enol. Vitic. 16 (3), 144–158.

Souto, X.C., Chiapusio, G., Pellissier, F., 2000. Relationships between phenolics and soil microorganisms in spruce forests: significance for natural regeneration. J. Chem. Ecol. 26 (9), 2025–2034.

Spigno, G., Tramelli, L., De Faveri, D.M., 2007. Effects of extraction time, temperature and solvent on concentration and antioxidant activity of grape marc phenolics. J. Food Eng. 81 (1), 200–208.

Standish, R.J., Williams, P.A., Robertson, A.W., Scott, N.A., Hedderley, D.I., 2004. Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants. Biol. Invasions 6 (1), 71–81.

Steinsiek, J.W., Oliver, L.R., Collins, F.C., 1982. Allelopathic potential of wheat (Triticum aestium) straw on selected weed species. Weed Sci. 30 (5), 495–497.

Stevens, R.J., Laughlin, R.J., Malone, J.P., 1998. Soil pH affects the processes reducing nitrate to nitrous oxide and di-nitrogen. Soil Biol. Biochem. 30 (8-9), 1119–1126.

Teuben, A., 1991. Nutrient availability and interactions between soil arthropods and microorganisms during decomposition of coniferous litter: a mesocosm study. Biol. Fertil. Soils 10 (4), 256–266.

Thomas, P.B., Possingham, H., Roush, R., 2005. Effects of boneseed (Chrysanthemoides monilifera (L.) Norl. ssp. monilifera) on the composition of the vegetation and the soil seed bank of an open eucalypt woodland. Plant Prot. Q. 20 (2), 74–80.

Thornley, J., Cannell, M., 2001. Soil carbon storage response to temperature: an hypothesis. Ann. Bot. 87 (5), 591–598.

Thorp, J., Lynch, R., 2000. The Determination of Weeds of National Significance. National Weeds Strategy Executive Committee, Launceston, Australia.

Uddin, M.N., Caridi, D., Robinson, R.W., 2012. Phytotoxic evaluation of *Phragmites australis*: an investigation of aqueous extracts of different organs. Mar. Freshw. Res. 63 (9), 777–787.

Uddin, M.N., Robinson, R.W., Caridi, D., Al Harun, M.A.Y., 2014a. Suppression of native *Melaleuca ericifolia* by the invasive *Phragmites australis* through allelopathic root exudates. Am. J. Bot. 101 (3), 479–487.

Uddin, M.N., Robinson, R.W., Caridi, D., Harun, M.A.Y., 2014b. Is phytotoxicity of *Phragmites australis* residue influenced by decomposition condition, time and density? Mar. Freshw. Res. 65 (6), 505–516.

Unger, I.M., Muzika, R.-M., Motavalli, P.P., 2010. The effect of flooding and residue incorporation on soil chemistry, germination and seedling growth. Environ. Exp. Bot. 69 (2), 113–120.

Van Vuuren, M., Aerts, E., Berendse, F., De Visser, W., 1992. Nitrogen mineralization in heathland ecosystems dominated by different plant species. Biogeochemistry 16 (3), 151–166.

Vranjic, J.A., Woods, M.J., Barnard, J., 2000. Soil-mediated effects on germination and seedling growth of coastal wattle (*Acacia sophorae*) by the environmental weed, bitou bush (*Chrysanthemoides monilifera* ssp. *rotundata*). Aust. Ecol. 25 (5), 445–453.

Wedin, D.A., Tilman, D., 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84 (4), 433–441.

Weiss, P.W., Adair, R.J., Edwards, P.B., 1998. *Chrysanthemoides monilifera* (L.) T. Norl. Biol. Aust. Weeds 2, 49–62.

Weiss, P.W., Adair, R.J., Edwards, P.B., Winkler, M.A., Downey, P.O., 2008. *Chrysanthemoides monilifera* subsp. *monilifera* (L.) T. Norl. and subsp. *rotundata* (DC.) T. Norl. Plant Prot. Q. 23 (1), 3–14.

Xiong, S.J., Nilsson, C., 2001. The effects of plant litter on vegetation: a meta-analysis. J. Ecol. 87 (6), 984–994.

Yamamoto, Y., 1995. Allelopathic potential of *Anthoxanthum odoratum* for invading Zoysia-grassland in Japan. J. Chem. Ecol. 21 (9), 1365–1373.