

Allelopathy: a tool for weed management in forest restoration

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Abstract Forest restoration uses active management to re-establish natural forest habitat after disturbance. However, competition from early successional species, often aggressively invasive exotic plant species, can inhibit tree establishment and forest regeneration. Ideally, restoration ecologists can plant native tree species that not only establish and grow rapidly, but also suppress exotic competitors. Allelopathy may be a key mechanism by which some native trees could reduce the abundance and impact of exotic species. Allelopathy is a recognized tool for weed management in agriculture and agroforestry, but few studies have considered how allelopathic interactions may aid restoration. Here we introduce the “Homeland Security” hypothesis, which posits that some naïve exotic species may be particularly sensitive to allelochemicals produced by native species, providing a tool to reduce the growth and impacts of invasive exotic species on reforestation. This article explores how

exploiting allelopathy in native species could improve restoration success and the re-establishment of natural successional dynamics. We review the evidence for allelopathy in agroforestry systems, and consider its relevance for reforestation. We then illustrate the potential for this approach with a case study of tropical forest restoration in Panama. C_4 grasses heavily invade deforested areas in the Panama Canal watershed, especially *Saccharum spontaneum* L. We measured the effect of leaf litter from 17 potential restoration tree species on the growth of invasive C_4 grasses. We found that leaf litter from legume trees had a greater inhibitory effect on performance of *S. spontaneum* than did litter from non-legume trees. However, allelopathic effects varied greatly among species within tree functional groups. Further evaluation of intra- and inter-specific interactions will help to improve our selection of restoration species.

Keywords *Saccharum spontaneum* · Legumes · Novel weapons hypothesis · Homeland security hypothesis · Allelopathy · Forest restoration

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Introduction

Anthropogenic disturbance of natural ecosystems is one of the biggest threats to biodiversity (Vitousek et al. 1994, 1997; Zhang and Fu 2009), and impacts are often exacerbated when disturbance facilitates invasion by exotic species (Mack et al. 2000).

For example, the intentional conversion of tropical forest to pastures of exotic grasses to raise cattle led to the subsequent colonization and spread of exotic C_4 grasses throughout disturbed areas in the new world tropics (Carpenter et al. 2004; Condit et al. 2001; D'Antonio and Vitousek 1992; Parsons 1972). Establishment of exotic C_4 grasses tends to be limited to disturbed habitats (Hooper et al. 2004; Leung et al. 2009; MacDonald 2004). Lack of establishment in forests may be limited by abiotic factors and biotic interactions with native species (Hou et al. 2011, 2012). Identifying traits of native species that impede invasion by exotic species may be useful when attempting to protect disturbed areas from invasion or restore them to forest.

Forest restoration attempts to return a disturbed area to a historical forest state. This includes the re-establishment of successional dynamics, nutrient and hydrological cycles, native species diversity, habitat connectivity, ecosystem services (Aerts and Honnay 2011; Clewell and Aronson 2006; Little and Lara 2010; Palmer et al. 1997; Satake and Rudel 2007; Young 2000), and increased carbon sequestration (Huang et al. 2012). Global initiatives such as REDD (www.unredd.org) that offer financial incentives for countries to restore and maintain forest cover have prompted research to improve the efficiency and efficacy of forest restoration techniques (Donald and Evans 2006; Putz and Redford 2010; Thangata and Hildebrand 2012).

Much of restoration ecology focuses on overcoming critical barriers to succession such as seed dispersal (Holl 1999; Murray et al. 2008; Wunderle 1997), abiotic factors (Loik and Holl 1999, 2001; McNamara et al. 2006; VanDuren et al. 1997), and identification of species that establish and grow rapidly in degraded environments (Chazdon 2003; Hall et al. 2011a, 2011b; Hooper et al. 2002, 2005; Jones et al. 2004; Nepstad et al. 1996; Park et al. 2010; van Breugel et al. 2011; Wishnie et al. 2007). Weedy exotic plants and other aggressive early successional species are important barriers to reforestation. Such species can delay or prevent succession from continuing to a desired restoration end point (Aide and Cavelier 1994; Aide et al. 1995, 2000; Chazdon 2003; Guariguata and Ostertag 2001; Hobbs and Huenneke 1992; Nepstad et al. 1996). For example, exotic C_4 grasses can prevent recolonization by native species in disturbed tropical forest landscapes (Hooper et al. 2004;

Jones et al. 2004). Removal of forests and increased light conditions that favor growth rates of C_4 grasses can lead to dense stands of these exotic invaders (Foxcroft et al. 2010; Joo Kim et al. 2008; Sage and Kubien 2003). Such invaders can further alter the natural successional trajectory if they generate feedbacks such as intensified fire regimes (Aide and Cavelier 1994; D'Antonio and Vitousek 1992). Reducing the abundance of invasive grasses is then critical to decrease fuel loads and allow the establishment of trees in the system. Since mechanical or chemical weed control can be prohibitively expensive, successful restoration may sometimes depend on the ability of planted species themselves to suppress exotic weeds (Hooper E. et al. 2002; Jones et al. 2004; Wishnie et al. 2007).

Certain functional traits may be key to the success of restoration species. Trees that rapidly produce deep shade may outcompete shade-intolerant exotic species (Jones et al. 2004; Joo Kim et al. 2008). Some planted trees can also affect growth of understory plants through their effects on nutrient availability (Ashton et al. 2008; Dakora and Phillips 2002; Pearson and Vitousek 2001) and soil pH (Haynes 1983). Less explored, however, is whether some tree species produce allelochemicals that inhibit germination or growth of understory plants. Native species that produce allelopathic compounds may be useful to control exotic weeds as part of forest restoration efforts.

In this paper we explore the potential use of allelopathy as a tool in forest restoration and exotic species management. We begin by reviewing literature from agroforestry and summarizing the approaches taken and evidence provided for allelopathic effects of trees on herbaceous weeds and crops. We then focus on allelopathy in the context of invasive species, examining situations where allelopathic species and response species do not share an evolutionary history. Finally, we present data from a greenhouse study that tests the allelopathic potential of leaves from trees used for forest restoration to suppress the growth of the exotic invasive grass *Saccharum spontaneum* L.

Allelopathy and agroforestry

Agroforestry is an approach to sustainable land management that integrates trees with agricultural crops and/or livestock (Rizvi et al. 1999). Inhibition of understory

growth in the absence of competition for light, water, or nutrients suggests that allelopathy may play a role in suppressing growth of some plants in the agroforest understory (Bhatt et al. 1997, 2010; Chou and Kuo 1986; Lodhi and Rice 1971). For example, black walnut (*Juglans nigra* L.) is commonly grown for its nuts and wood in North America. Sensitivity of understory crops to allelochemicals produced by *Juglans* spp. has required careful evaluation of which species can be effectively incorporated into *Juglans* agroforestry models (Willis 2000). Similar interactions in other intercropping systems have stimulated interest in determining optimal crop/tree combinations. In addition to the interspecific allelopathic effects of agroforestry trees on understory crops, some studies have documented inhibitory allelopathic effects of trees on weed germination and growth (Babu and Kandasamy 1997; Chou and Kuo 1986; Kaur et al. 2011; Matok et al. 2009; Williams and Hoagland 2007; Wu et al. 2011).

Allelopathy has been suspected in a wide range of tree species (Table 1). In addition to *Juglans* (walnut), the allelopathic effects of numerous agroforestry genera, including *Eucalyptus* spp. (Espinosa-Garcia 1996) and *Leucaena* spp. (John and Narwal 2003), have been particularly well studied (Table 1). Robust conclusions about the importance of allelopathic interactions in field systems require extensive and interlinked experimental bioassays, biochemical characterization, and field experiments (Inderjit and Callaway 2003). Unfortunately, there are few data available to evaluate allelopathic activity for most suspected species (Table 1).

The Petri dish bioassay of leaf extracts (leachates) on seed germination and seedling growth is perhaps the most common approach to studying allelopathy. Many studies (Table 1) that used leaf extract bioassays found a negative effect of tree leaf material on crop seedlings (Bhatt et al. 2010; Cui et al. 2011; Lisanework and Michelsen 1993). However, the most consistent result is a tremendous variation among response species in their degree of susceptibility to extracts (Table 1).

There are fewer studies that measure natural levels of allelochemicals in the soil or that quantify the allelopathic effects of trees on herbaceous plants in the field (Table 1). Singh and Kohli (1992) found that crops grown closer to *Eucalyptus* shelterbelts (wind-break plantations) had reduced yields, and that soil extracts from near *Eucalyptus* suppressed germination. More field studies are needed to quantify the strength

of allelopathic effects of trees on crops and other herbaceous species.

The combined results of these studies have stimulated interest in the use of allelopathic trees as part of crop production and pest management systems. Depending on the crop-tree (Alrababah et al. 2009; Chaturvedi and Jha 1992; Li et al. 2010b; Lisanework and Michelsen 1993) or weed-tree (Babu and Kandasamy 1997; El-Rokiek and Eid 2009; Kaur et al. 2011) combination, the effect of tree allelochemicals may vary from inhibitory to stimulatory. For example, when investigating the effects of leaf extracts on two perennial weeds, fresh leaf leachates of *Eucalyptus globulus* Labill. inhibited the growth of bermuda grass (*Cynodon dactylon* L. Pers.) but promoted the growth of purple nutsedge (*Cyperus rotundus* L.) (Babu and Kandasamy 1997). Similarly, germination of cereal crops was less affected than legume crops by fresh and dry leaf extracts and soil extracts from *Quercus coccoifera* L. and *Pinus halpensis* Mill. (Alrababah et al. 2009). This demonstrates the need for careful evaluation of tree-crop/weed combinations when designing agroforestry systems.

Understanding the mechanisms of differential allelopathic effects can open opportunities for creative forest restoration and agroforestry management, by excluding recruitment of undesired species while promoting others. *Terminalia* spp. (Baratelli et al. 2012; Bhatt et al. 1997, 2010), *Gliricidia sepium* (Jacq.) Kunth. (John et al. 2007; Kamara et al. 2000a, 2000b; Williams and Hoagland 2007), and *Tectona grandis* (Linn. f.) (Bhatt et al. 2010; John et al. 2007; Sahoo et al. 2007) have been suggested to be allelopathic toward crops and weeds, and are also used commonly for restoration (Wishnie et al. 2007; van Breugel et al. 2011). These studies point to possible strategic uses of allelopathic trees in restoration or forestry. Here we explore the idea of incorporating these concepts into forest restoration models to improve restoration in areas where invasive weeds inhibit restoration success.

Resisting invasion and restoration: the “Homeland Security” hypothesis

Some aggressive invaders are thought to be successful in part because of allelochemicals they produce. A number of invasive species are thought to have

Table 1 Representative studies investigating allelopathy of trees on understory plants

Tree taxon	Response species	Type of response spp.	Approach	Main result	Citation	Location
<i>Juglans regia</i>	<i>Atractylodes macrocephala</i> , <i>Isatis tinctoria</i> , <i>Polygala tenuifolia</i> , <i>Salvia mitirrhiza</i>	Medicinal plants	Effect of leaf extracts on seed germination	Variation among response species	(Li et al. 2010b)	China
<i>Juglans regia</i>	Turnip (<i>Brassica rapa</i>)	Crops	Effect of leaf extracts on germination and growth	Older trees produced stronger effects	(Cui et al. 2011)	China
<i>Juglans regia</i>	Dandelions (<i>Taraxacum officinale</i>)	Weed	Effects of extracts of fallen leaves, husks, and roots on seed germination and growth	Reduced germination	(Matok et al. 2009)	Poland
<i>Juglans regia</i> , <i>Pinus</i> spp.	Bread wheat (<i>Triticum aestivum</i>)	Crop	Field experiment: leaf and extract effects on growth	Reduced grain yield	(Akkaya et al. 2006)	Turkey
<i>Pinus halepensis</i> , <i>Quercus coccifera</i>	Wheat (<i>Triticum aestivum</i>), barley (<i>Hordeum vulgare</i>), lentil (<i>Lens culinaris</i>), chickpea (<i>Cicer arietinum</i>), fava bean (<i>Vicia faba</i>)	Crops	Effects of leaf extracts on germination	Legume crop germination was more sensitive to extracts than cereal crops	(Alrababah et al. 2009)	Jordan
<i>Cupressus lusitanica</i> , <i>Eucalyptus globulus</i> , <i>Eucalyptus camaldulensis</i> , <i>Eucalyptus saligna</i>	Chickpea (<i>Cicer arietinum</i>), maize (<i>Zea mays</i>), pea (<i>Pisum sativum</i>), teff (<i>Eragrostis tef</i>)	Crop	Effects of leaf extracts on germination and seedling growth	Reduced germination and growth. Effects of <i>C. lusitanica</i> < <i>E. globulus</i> < <i>E. saligna</i> < <i>E. camaldulensi</i>	(Lisanework and Michelsen 1993)	Ethiopia
<i>Eucalyptus tereticornis</i>	Chickpea (<i>Cicer arietinum</i>), lentil (<i>Lens esculentum</i>), wheat (<i>Triticum aestivum</i>), cauliflower (<i>Brassica oleracea</i>), toria (<i>Brassica campestris</i>), Beerseem Clover (<i>Trifolium alexandrinum</i>)	Crop	Distance from shelterbelts (windbreak plantations in agricultural landscapes) as a proxy for chemical influence on the soil	Bioassays showed negative effects of soil extracts close to the shelterbelt, crop yield increased with distance	(Singh and Kohli 1992)	India
<i>Eucalyptus urophylla</i>	<i>Delonix regia</i> , <i>Eleocarpus sylvestris</i> , <i>Schima superba</i> , <i>Michelia macclurei</i>	Native spp.	Factorial field experiment manipulating the presence of roots and litter	Germination was depressed in the presence of <i>Eucalyptus</i> roots or litter. Seedling growth was reduced with roots but not litter	(Zhang and Fu 2009)	China
<i>Eucalyptus camaldulensis</i>	Spinach (<i>Spinacia oleracea</i>), onion (<i>Allium cepa</i>), garden cress (<i>Lepidium sativum</i>), barnyard grass (<i>Rumex acetosella</i>), maize (<i>Zea mays</i>), tomato (<i>Solanum lycopersicon</i>), wild oat (<i>Avena fatua</i>)	Crops and weeds	Effects of leaf and volatile oil extracts on the Hill reaction in chloroplasts (spinach), mitosis (onion), meristematic root tips and radical growth, and peroxidase activity (all other spp.)	Decreased cell division in the root apical meristem (<i>A. cepa</i>), inhibition of the Hill reaction (spinach), reduction in radical growth across all other spp. except <i>Z. mays</i>	(Moradshahi et al. 2003)	Iran
<i>Eucalyptus citriodora</i>	<i>Avena fatua</i> , <i>Hippeastrum hybridum</i>	Weeds	Effect of leaf extracts on growth and germination of oat weed. Greenhouse study of leaf extracts on oat weed and amaryllis growth and flowering	Inhibition of oat weed in lab and greenhouse. Stimulation of <i>Amaryllis</i> growth	(El-Rokiek and Eid 2009)	Egypt
<i>Eucalyptus dundasii</i>	<i>Lolium rigidum</i> , <i>Hordeum glaucum</i>	Weeds	Extract and Oil fraction effects on germination and growth	Oils depressed germination and sometimes growth	(Wu et al. 2011)	Australia

Table 1 continued

Tree taxon	Response species	Type of response spp.	Approach	Main result	Citation	Location
<i>Eucalyptus globulus</i>	<i>Cyperus rotundus</i> , <i>Cynodon dactylon</i>	Weeds	Greenhouse bioassay of fresh and dry leaf extract and fresh leaf cuttings on germination and growth	Fresh extracts inhibited bermuda grass but promoted purple nutsedge. Dry leaf extract had differential effects	(Babu and Kandasamy 1997)	India
<i>Eucalyptus</i> spp., <i>Acacia auriculiformis</i>	Rice (<i>Oryza sativa</i> var. Moroberekan)	Crop	Effects of leaf litter extracts on young rice seedlings	Increase in the root weight/ root length ratio	(Bernhard-Reversat 1999)	Congo
<i>Eucalyptus tereticornis</i>	<i>Amaranthus viridis</i>	Weed	Chemical composition and effect of volatile oils on seed germination and seedling growth	Reduced seedling growth, photosynthesis, and energy metabolism	(Kaur et al. 2011)	India
<i>Eucalyptus urophylla</i>	Native trees: <i>Cinnamomum burmanni</i> , <i>Cryptocarya concinna</i> , <i>Machilus chinensis</i> , <i>Photinia benthamiana</i> , <i>Pygeum topengii</i> , <i>Diospyros morrisiana</i> , <i>Pterospermum lanceaefolium</i> ; Exotic trees: <i>Acacia confusa</i> , <i>Albizia lebbek</i> , <i>Albizia falcataria</i>	Native and exotic trees	Effects of leaf extracts and volatiles on seed germination and seedling growth	Variation among response species and response variables	(Fang et al. 2009)	China
<i>Chukrasia tabularis</i> , <i>Tectona grandis</i> , <i>Terminalia myriocarpa</i> , <i>Trema orientalis</i>	Rice (<i>Oryza sativa</i>), maize (<i>Zea mays</i>), <i>Vigna radiata</i> , <i>Vigna umbellata</i> , <i>Arachis hypogea</i> , <i>Brassica campestris</i>	Crops	Effects of leaf extracts on germination and on growth in pots	Response species varied: Oilseed crops were most susceptible, followed by cereal crops and finally legumes	(Bhatt et al. 2010)	India
<i>Pinus pinea</i>	<i>Cistus salvifolius</i> , <i>Cistus libanotis</i> , <i>Halimium halimifolium</i>	Native shrubs	Needle extracts crossed with a physical barrier (toothpicks) treatment	Extracts reduced germination; responses varied across shrub species	(Valera-Burgos et al. 2012)	Spain
<i>Pinus massoniana</i> , <i>Schima superba</i> , <i>Castanopsis chinensis</i> , <i>Castanopsis fissa</i> , <i>Cryptocarya chinensis</i> , <i>Cryptocarya concinna</i>	<i>Mikania micrantha</i>	Weed	Leaf litter extract bioassays, 5-mo. pot experiment using 5 of the 6 spp.	Extracts from all spp. reduced early growth. Tree seedlings suppressed the invader in four cases but not in one for the pot experiment	(Hou et al. 2012)	China
<i>Gliricidia sepium</i> , <i>Diphysa americana</i> , <i>Inga punctata</i> , <i>Tectona grandis</i> , <i>Pachira quinata</i> , <i>Terminalia amazonia</i>	<i>Saccharum spontaneum</i>	Weed	Leaf litter addition in pot experiment	Effect of litter on survival was negative with legume trees but not with non-legumes	Cummings et al. (this paper)	Panama
17 tree species (see Fig. 2)	<i>Saccharum spontaneum</i>	Weed	Leaf litter addition in pot experiment	Overall effect of litter on growth positive; with legume trees, less positive than non-legumes	Cummings et al. (this paper)	Panama
<i>Acacia delbata</i>	Lettuce (<i>Lactuca sativa</i>), maize (<i>Zea mays</i>), <i>Dactylis glomerata</i> , <i>Arabidopsis thaliana</i> , <i>Acacia delbata</i>	Crops, herbs, and tree spp.	Throughfall and litter extract effects on seed germination and seedling growth	Differential effects on test spp. with mostly stimulatory effects	(Lorenzo et al. 2010)	Spain

Table 1 continued

Tree taxon	Response species	Type of response spp.	Approach	Main result	Citation	Location
<i>Acacia melanoxylon</i> , <i>Quercus robur</i> , <i>Pinus radiata</i> , <i>Eucalyptus globulus</i>	Lettuce (<i>Lactuca sativa</i>)	Crop	Effects of extracts of decomposing leaf material on germination	Inhibitory effects varied by species and with time	(Gonzales et al. 1995)	Spain
<i>Acacia melanoxylon</i>	Cocksfoot (<i>Dactylis glomerata</i>) ryegrass (<i>Lolium perenne</i>), common sorrel (<i>Rumex acetosa</i>), lettuce (<i>Lactuca sativa</i>)	Native spp. and lettuce	Effects of phylode and flower extracts on germination and physiological function in perlite	Reduction in growth and physiological function in all spp.	(Hussain et al. 2011)	Spain
American chestnut (<i>Castanea dentate</i>)	Red maple (<i>Acer rubrum</i>), sugar maple (<i>A. saccharum</i>), eastern white pine (<i>Pinus strobus</i>), eastern hemlock (<i>Tsuga canadensis</i>), yellow-poplar (<i>Liriodendron tulipifera</i>), rosebay rhododendron (<i>Rhododendron maximum</i>), lettuce (<i>Lactuca sativa</i>)	Native trees and lettuce	Extract effects on seed germination and seedling growth	Reduction in germination and radical growth	(Vandermast et al. 2002)	USA
<i>Celtis laevigata</i>	<i>Andropogon gerardi</i> , <i>A. scoparius</i> , <i>Panicum virgatum</i> , <i>Sorghastrum nutans</i>	Native spp.	Field study comparing stands of <i>C. laevigata</i> and <i>Prunus</i> ; Greenhouse experiment on effects of dried leaf litter, extracts, and soil on germination and growth	Inhibitory effects of decaying leaves, extracts, and soils	(Lodhi and Rice 1971)	USA
<i>Leucaena leucocephala</i>	Rice (<i>Oryza sativa</i>), <i>Acacia niolotica</i> , <i>Casuarina equisetifolia</i> , <i>Pongamia pinnata</i> , <i>Lagerstroemia speciosa</i> , <i>Sesbania grandiflora</i> , <i>Leucaena leucocephala</i>	Crop (rice) and tree spp.	Effects of leaf extracts on germination and growth. Evaluation of mimosine content in leaves of <i>Leucaena</i>	Variation in mimosine content between varieties. Differential germination among test species	(Chaturvedi and Jha 1992)	India
<i>Eucalyptus camaldulensis</i> ,	<i>Amaranthus hybridus</i> , <i>Portulaca oleracea</i>	Weeds	Oil extraction and effects on seedling growth and germination	Complete inhibition of germination and seedling growth	(Verdeguer et al. 2009)	Spain
<i>Leucaena leucocephala</i>	Lettuce (<i>Lactuca sativa</i>), rice (<i>Oryza sativa</i>), rye grass (<i>Lolium multiflorum</i>), <i>Acacia confusa</i> , <i>Alnus formosana</i> , <i>Casuarina glauca</i> , <i>Pinus taiwanensis</i> , <i>Liquidambar formosana</i> , <i>Miscanthus floridulus</i> , <i>Mimosa pudica</i> , <i>Ageratum conyzoides</i>	Crops, weeds, and trees	Comparison of understory biomass between <i>Leucaena</i> and grasslands. Seedling response to dry leaf extracts and to soil from beneath <i>Leucaena</i> .	Lower biomass under <i>Leucaena</i> . Extracts reduced germination and growth of all test spp except <i>P. taiwanensis</i> and <i>M. floridulus</i>	(Chou and Kuo 1986)	Taiwan

Table 1 continued

Tree taxon	Response species	Type of response	Approach	Main result	Citation	Location
<i>Leucaena leucocephala</i> , <i>Gliricidia sepium</i> , <i>Senna siamea</i>	Talinum triangulare Sedges (Cyperus and Mariscus spp.), Panicum maximum, Digitaria horizontalis, Triumfetta spp., Chromolaena odorata, Centrosema pubescens, Celosia leptostachya, Calopogonium mucunoides, Commelina spp., Physalis angulata, Desmodium scorpirus, Oldenlandia corymbosa, Tridax procumbens, Psophocarpus palustris, Euphorbia hirta, other grass weeds, other broadleaf weeds	Weeds	Field experiment: mulch suppression of local weeds	Mulch from <i>G. sepium</i> and <i>S. siamea</i> suppressed weed growth, but no effect of <i>L. leucocephala</i>	(Kamara et al. 2000a)	Nigeria
<i>Sonneratia apetala</i> , <i>Spartina alterniflora</i>	Alfalfa (<i>Medicago sativa</i>), ryegrass (<i>Lolium perenne</i>), sudangrass (<i>Sorghum sudanense</i>)	Weeds and crops	Effect of leaf volatiles and soil on germination and growth	Volatiles reduced germination and growth. Soil from <i>S. apetala</i> suppressed <i>S. alterniflora</i> growth	(Li et al. 2010a)	China

For each study, we report: the putatively allelopathic tree species that was the focal species for the investigation, the species that were measured for their response to allelopathy, the classification of the type of response species, the type of approach taken in the study, a briefly stated main result of the study, the citation, and the location of the study. Unless otherwise stated, effects were measured in petri plate bioassays

allelopathic properties (Haubensak and Parker 2004; Inderjit et al. 2006; Jarchow and Cook 2009; Lankau 2010; Valera-Burgos et al. 2012; Wink 2002); however, it is not clear how often allelopathy contributes to invasion success. Allelochemicals produced by introduced species may facilitate invasion when native species cannot tolerate what to them are novel chemical compounds (Bais et al. 2003; Callaway and Ridenour 2004; Pollock et al. 2008). The novel weapons hypothesis (Callaway and Ridenour 2004) suggests that an introduced species may have strong allelopathic effects on neighboring plant species in a novel environment, even though it does not show similar effects on species in its native range where plants share an evolutionary history. For instance, competitive dominance of *Centaurea diffusa* Lam. in invaded range of North America has been attributed to the release of allelopathic compounds into the environment (Callaway and Aschehoug 2000; Ridenour and Callaway 2001). Studies using the congener *Centaurea maculosa* Lam. (now *C. stoebe*) showed similar negative allelopathic effects on plant species in its invaded range of North America (He et al. 2009; Thorpe et al. 2009). Increasing evidence suggests that,

for some species, allelopathy may play a major role in invasion success.

The concept of “novel weapons” could also operate in reverse to increase the resistance of native communities to invasion. We call this the “Homeland Security” hypothesis. Introduced plants may be naïve and particularly susceptible to allelochemicals produced by local native plant species, which could impede invasion. Thus allelopathy may contribute to invasion resistance of native communities. For example, in Florida’s sand pine scrub habitats, allelochemicals released by *Polygonella myriophylla* (Small. Horton) and other native scrub vegetation inhibit invasion by invasive grasses such as bahiagrass *Paspalum notatum* (Small) Horton (Weidenhamer and Romeo 2005).

Variation in allelopathy of native plant species may also contribute to variation in invasibility across plant communities. *Mikania micrantha* H.B.K. is a highly invasive perennial vine that has spread widely throughout China, invading forests and agricultural areas (Hou et al. 2012). Variation in *M. micrantha* invasion success raised the question of whether allelopathy from certain local trees might suppress growth of the exotic.

Hou et al. (2012) tested the allelopathic response of *M. micrantha* to six dominant tree species: *Pinus massoniana* Lamb., *Schima superba* (Gardner & Champ), *Castanopsis chinensis*, *Castanopsis fissa*, *Cryptocarya chinensis* (Hance) Hemsl, and *Cryptocarya concinna* (Hance) Hemsl from 3 different forest types. All six tree species inhibited root growth after germination in laboratory bioassays using leaf litter extracts. In a pot experiment, individual seedlings of five of the tree species were planted in pots with 50 seeds of *M. micrantha* and grown for 5 months. Growth of *M. micrantha* was inhibited by four of the species, while one (*C. concinna*) enhanced stem length and biomass (Hou et al. 2012). This study suggests that invasion resistance of intact communities may be partially due to allelochemical growth inhibition of exotic species. However, we need more studies that examine the interactions between potentially allelopathic natives and exotic species.

Evaluating which native species may provide an allelopathic arsenal against invaders currently requires a species-by-species, empirical approach. Assessing the usefulness of functional groups for predicting allelopathy is especially important in tropical forest restoration, where hyperdiverse native communities offer hundreds of tree species as possible choices. For example, fast-growing pioneer species in areas with high resource availability tend not to invest heavily in secondary chemistry (Fine et al. 2006), and may be less likely to have allelopathic effects. Certain families or genera are associated with high concentrations or high diversity of secondary compounds that could produce allelopathic effects (Hadacek 2002; Singh et al. 2003; Wink 2003). For instance, the high levels of glucosinolates found in many Brassicaceae and alkaloids in many Fabaceae may increase the probability that plants in these groups could have allelopathic effects.

Incorporating allelopathy into forest restoration strategies: a case study from Panama

In many parts of the tropics, weedy C₄ grasses colonize degraded deforested areas (Batianoff and Franks 1998; Hooper et al. 2004; Jones et al. 2004; Nepstad et al. 1996; Wishnie et al. 2007). In Panama, *S. spontaneum* (hereafter *Saccharum*) is a large exotic grass species that invades abandoned agricultural

fields and other disturbed sites. Like other C₄ grasses, *Saccharum* is adapted to drought, establishes and grows rapidly in high light conditions, and promotes intense and frequent fires that kill young trees. It is very difficult to eradicate and is considered one of the most serious weeds in many tropical areas (Holm et al. 1979; Hooper et al. 2004).

In Panama, PRORENA (The Native Species Reforestation Program) has examined numerous strategies for inhibiting *Saccharum* and restoring diverse, native tropical forests. In an abandoned agricultural area dominated by *Saccharum*, PRORENA established replicated monospecific reforestation test plots to evaluate survival, growth, and canopy cover of over 75 different native and commercially important tree species (Hall et al. 2011b; Hooper et al. 2002; Jones et al. 2004; Park et al. 2010; van Breugel et al. 2011; Wishnie et al. 2007). In previous work, these species were characterized for a number of functional traits, but not for allelopathic effects.

We observed great variation in the density and growth of *Saccharum* under different tree species in the PRORENA plots. Not surprisingly, density of the invader was lower in deep shade, but it was even lower under legume than under non-legume tree species (Cummings, unpublished data). These observations led to the hypothesis that allelopathic effects of legumes might contribute to suppression of *Saccharum*.

Because litter decomposition can be an important source of allelochemicals (Reigosa et al. 1999), we focused on the effects of leaf litter from legume and non-legume trees on growth of *Saccharum*. Leaf litter would be expected to deliver nutrients to the plants as well, meaning that allelopathic effects can be modulated by other factors in litter addition studies. However, from a practical perspective, litter addition is a sensible first step to evaluate whether a candidate species for restoration might help control weeds (Babu and Kandasamy 1997). In a shade house, we placed 4 g of fresh mature leaves from three legumes, (*Gliricidia sepium*, *Diphysa americana* (Mill.) M. Sousa, and *Inga punctata* Willd.), three non-legume (*Tectona grandis* L. f., *Pachira quinata* (Jacq.) W.S. Alverson, and *Terminalia amazonia* (J.F.Gmel.)), all tree species from the PRORENA plots, on the surface of nursery bags containing potting soil and test plants of *Saccharum* ($n = 15$ per tree species). Asexually produced *Saccharum* tillers were removed from the maternal plant and planted in the bags containing soil

just prior to placing leaves on the soil surface. We included a control group that was identical to our treatments except that no leaves were added to the bags. This project was established at the end of May 2011 and harvested after 7 weeks. Bags were surface-watered during this time to allow for the breakdown of leaf material and release of compounds. We used a nested ANOVA (species within functional groups) to compare performance measures (leaf node height, above- and below-ground biomass, and mortality) at harvest, and general linear models with binomial variables for mortality. Results of the control treatments are presented graphically, but are not included in statistical analyses because the nested structure (species within legume/non-legume) could not easily incorporate a comparison to the control (which was not replicated in the same way as functional group). However, the controls serve as a reference in the figures to evaluate the net of positive and negative effects of leaves from legume and non-legume trees. All data were analyzed using the statistical program R version 2.14.0.

Survival of *Saccharum* was significantly reduced by applying leaves of legume overstorey species compared to non-legume leaves (Fig. 1a). Change in height was also marginally lower when leaves were from legume trees (Fig. 1b). Above-ground ($F = 0.64$; $df = 2,4$; $p = 0.62$) and below-ground ($F = 0.73$; $df = 2,4$; $p = 0.49$) biomass was not significantly different. *Tectona grandis* did not show a strong negative effect on *Saccharum* (Fig. 1), which was surprising since leaf extracts of *T. grandis* have been shown to inhibit the germination, growth, and biomass yield of *Arachis hypogaea* L. and *Brassica campestris* L. (Bhatt et al. 2010).

We found that decomposing leaves from legumes appeared to reduce the persistence of *Saccharum*, but there was also much variation among legume tree species. We conducted a larger experiment with 17 candidate tree species, including 6 species of legume (*Gliricidia sepium*, *Inga punctata*, *Enterolobium cyclocarpum* (Jacq.) Griseb, *Diphysa americana* (Mill.) M. Sousa, *Albizia guachapeli* (Kunth), and *Albizia adenocephala*) and 11 species of non-legume trees (*Terminalia amazonica* (J.F. Gmel) Exell, *Tectona grandis*, *Tabebuia rosea* DC, *Tabebuia guayacan* (Seem.) Hemsl. *Pachira quinata* (Jacq.), *Ochroma pyramidale* (Cav. ex Lamk), *Luehea semanii* Planch. & Triana, *Guazuma ulmifolia* Lam, *Columbrina*

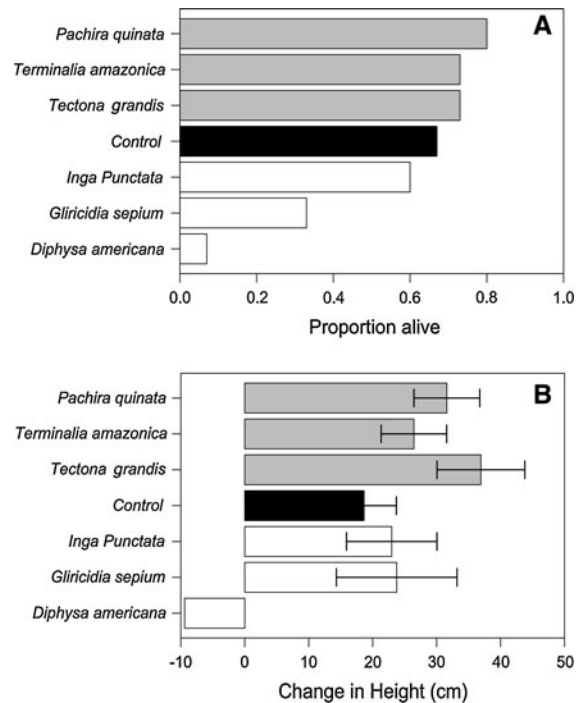


Fig. 1 **a** Survival of *Saccharum spontaneum* for 7 weeks was significantly less after applying litter from legume (white) than non-legume (gray) tree species ($df = 5$; $Z = 3.88$; $p < 0.001$). **b** Mean change in height (\pm S.E.) for *Saccharum* grown with litter from legume and non-legume overstorey trees. Legumes and non-legumes were marginally different ($df = 1,4$; $F = 2.95$; $p = 0.09$). Black bar is the no-litter control

glandulosa, *Cedrela odorata* L., and *Calycophyllum candidissimum* (Vahl.) DC) that were being evaluated as forest restoration species in the PRORENA plots. This project was implemented for 6 weeks from Oct–Nov 2011 with the same design to that above ($n = 15$ individuals per species). In this experiment, plants treated with litter from legume trees showed marginally lower above-ground biomass (Fig. 2a) and below-ground biomass (Fig. 2b), than those with non-legume litter; there was no effect of legumes ($Z = 0.38$; $df = 17$; $p = 0.70$) or non-legumes on mortality ($Z = 1.03$, $df = 17$; $p = 0.92$). Interestingly, application of non-legume litter resulted in significantly higher biomass than controls with no litter, suggesting a possible nutritional benefit from litter.

The two studies together suggest that different tree species and perhaps functional groups of trees will have different effects on *Saccharum*, beyond effects of direct competition and shading. These patterns could

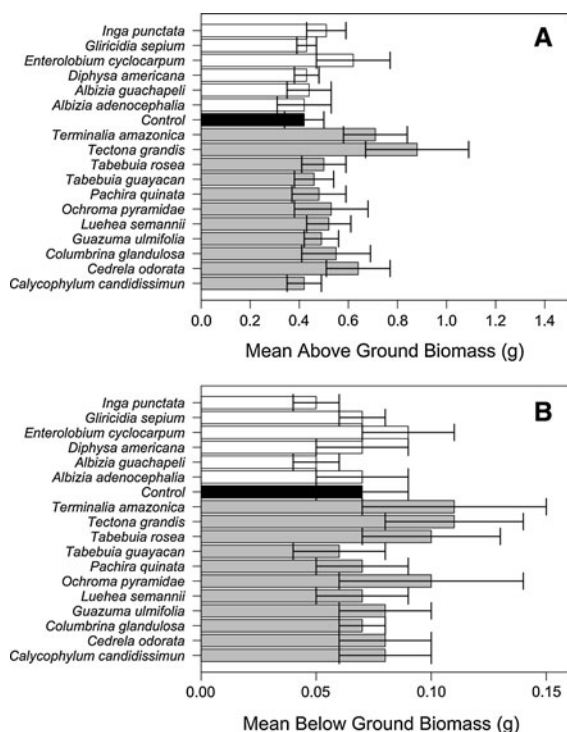


Fig. 2 **a** Mean (\pm S.E.) above-ground biomass ($df = 1,15$; $F = 3.45$; $p = 0.07$) and **b** mean (\pm S.E.) below-ground biomass ($df = 1,15$; $F = 3.45$; $p = 0.07$) of *Saccharum* grown in the shade house with litter from legume (white) and non-legume (gray) tree species. *Saccharum* biomass was marginally lower in legume treatments than non-legume treatments. No-leaf controls (black bars) are shown for visual comparison

be consistent with positive fertilization effects as well as negative allelopathic effects from canopy tree litter.

Future directions

The primary measure of forest restoration success is the survival and growth of focal tree species (Hall et al. 2011b; Jones et al. 2004; van Breugel et al. 2011; Wishnie et al. 2007). However, trees planted for restoration may also be able to suppress exotic weed species (Jones et al. 2004); this is particularly important when invasive exotic species promote fire that threatens long term forest recovery. Under these conditions, the allelopathic potential of native species should be assessed along with growth rates and other traits for evaluating restoration candidates.

Variation in the impact of restoration species on the performance of an invasive grass beyond that expected

from shade alone suggests that allelopathy may be a useful tool for forest restoration. While other studies suggest that the trees produce allelochemicals, we found fairly weak evidence for allelopathic effects on the grasses in this study; in some cases addition of tree litter even enhanced growth and survival of the grass. This suggests caution and particular attention to species-specific effects when recommending particular species for restoration.

Susceptibility to allelopathic chemicals can vary among recipient species (Bhatt et al. 2010; Caamal-Maldonado et al. 2001; Rizvi et al. 1999; Zhang and Fu 2010). The choice of restoration species may depend on which weeds are problems at a given site. We currently know little about how much variation to expect in the response of functionally similar species—among different tropical C_4 grasses, for example, to allelopathic litter. Thus, incorporating allelopathy into restoration strategies will require testing across response species to determine whether effects are general or species specific.

Stressful conditions can also amplify both the production and the effects of allelochemicals (Blanco 2007; Graneli and Salomon 2010; Hooper et al. 2009; Reigosa et al. 2006; Tesio and Ferrero 2010; Varkitzi et al. 2010). For example, N and P deficiency can enhance the production of allelochemicals in some species (Graneli and Salomon 2010; Varkitzi et al. 2010) as well as sensitivity to allelochemicals (Einhellig 1996). Water stress (Tang et al. 1995; Tongma et al. 2001) and interspecific competition (Lankau and Strauss 2007) can similarly stimulate the production of allelochemicals. In one study, stress effects were found to be the most intense when plants were exposed to a combination of allelochemicals, salt, and drought (Reigosa et al. 2006). In some cases, microbes enhance allelopathic effects by converting allelopathic compounds into more toxic forms (Bains et al. 2009; Gagliardo and Chilton 1992), or by redistributing allelochemicals through fungal networks (Barto et al. 2011). The stress of growing under low light, such as found in the PRORENA plots in Panama, can sometimes act synergistically with allelopathic chemicals (Hussain et al. 2011; Lorenzo et al. 2011). The combination of stressful conditions and allelopathy could thus work in conjunction to inhibit growth more than competition alone.

Plants species that share an evolutionary history with allelopathic species may have evolved resistance

to the allelochemicals that allow them to co-exist (Pollock et al. 2008; Thorpe et al. 2009; Vivanco et al. 2004). For example, the allelochemical (-) catechin, produced by the exotic invader *Centaurea maculosa*, reduced growth when applied to pots containing grasses from its invaded range of North America, but did not affect the growth of grasses from its native range (Bais et al. 2003). Other studies have found similar patterns where allelopathic species have neutral interactions with species from their native range, whereas they inhibit species with which they lack an evolutionary history (Callaway and Aschehoug 2000; Callaway et al. 2012; Kim and Lee 2011; Ni et al. 2010; Thorpe et al. 2009). Some allelochemicals can even promote the growth of species that share a coevolutionary history (Kim and Lee 2011). The Homeland Security hypothesis suggests that allelopathic effects may provide useful antagonistic tools early in restoration to provide an advantage to native species over exotics, but then gradually fade in importance as the restored sites are colonized by additional native species. Careful selection and monitoring of early restoration species not only for their growth characteristics but also for their ability to inhibit weedy exotics and favor native biodiversity may improve restoration success.

We recommend that to evaluate the utility of allelopathy, forest restoration studies should:

1. Monitor response of invader species to plantings of native tree species.
2. Examine interactions between candidate reforestation species and locally problematic weeds through extract, litter, and field experiments.
3. Monitor natural recruitment of native species under allelopathic restoration trees.
4. Investigate interactions between allelopathic effects and other stressors, including nutrients, drought, and light.

To test the “Homeland Security” hypothesis, studies using native species should quantify the relative importance of allelopathy effects on other natives versus allelopathy effects on introduced species. Ideally, these studies will go beyond leaf extract bioassays and will include evidence from field studies as well.

Based on the ecological role of allelopathy, and in keeping with the Homeland Security hypothesis, we propose that identifying and incorporating allelopathic

native species into restoration models may help to improve restoration by disproportionately suppressing invasive exotics. Research on forest restoration has greatly improved our ability to reforest degraded areas (Hall et al. 2011a, 2011b; Hooper et al. 2002; Wishnie et al. 2007). Allelopathy may be an additional useful tool to help reduce the persistence of exotic weeds and expedite the restoration of our world’s forests.

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