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Does carbon addition to soil counteract disturbance-promoted alien plant invasions?

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Abstract: Addition of carbon to the soil promotes microbial immobilization of plant-available nutrients, and is being considered as a method to counter alien plant invasions, particularly in disturbed habitats. In the present study the response of three confamilial alien invasive species, *Anthemis cotula*, *Conyza canadensis,* and *Galinsoga parviflora,* to independent and interactive effects of soil tillage (soil disturbance) and sawdust incorporation into soil (carbon addition) was investigated in terms of plant density, height, number of capitula per plant, and root, shoot and whole-plant dry mass. These attributes were favourably promoted by soil disturbance, particularly in *Anthemis cotula* and *Conyza canadensis*, but the magnitude of increase in different traits was highly species-specific. Addition of sawdust significantly reduced disturbance-mediated increase in most of the investigated traits. Despite differences in response of alien invasive species to soil manipulations, carbon addition could be used as a countermeasure to effectively combat some alien plant invasions.

Resumen: La adición de carbón al suelo promueve la inmovilización microbiana de nutrientes disponibles para las plantas y está siendo considerada como un método para contener las invasiones de plantas exóticas, particularmente en hábitats perturbados. En el presente estudio se investigó la respuesta de tres especies invasoras exóticas confamiliares, *Anthemis cotula, Conyza canadensis* y *Galinsoga parviflora*, a los efectos independientes e interactivos del arado del suelo (disturbio del suelo) y la incorporación de aserrín al suelo (adición de carbón), en términos de densidad de plantas, altura, número de capítulos por planta, y masa seca de la raíz, del vástago y de la planta completa. Estos atributos fueron promovidos favorablemente por el disturbio del suelo, particularmente en *Anthemis cotula* y *Conyza canadensis*, pero la magnitud del aumento de los diferentes rasgos fue claramente específica de la especie. La adición de aserrín redujo significativamente el incremento resultante del disturbio en la mayoría de los rasgos investigados. No obstante las diferencias en las respuestas de las especies invasoras exóticas a las manipulaciones del suelo, la adición de carbón podría ser usada como una medida de combate efectivo contra algunas invasiones de plantas exóticas.

Resumo: A adição de carbono no solo promove a imobilização microbiana dos nutrientes disponíveis, e tem sido considerado como um método para conter a invasão de plantas alieligenas, particularmente em habitats disturbados. No estudo presente, a resposta de três espécies exóticas confamiliares invasivas, a *Anthemis cotula*, a *Conyza canadensis*, e a *Galinsoga parviflora*, para provocar efeitos independentes e interactivos da lavoura do solo (distúrbio no solo), e da incorporação da serradura no mesmo (adição de carbono) foi investigada em termos da densidade das plantas, altura, número de capítulos por planta, raízes e massa seca de todas as plantas. Estes atributos foram promovidos favoravelmente pelo distúrbio do solo, particularmente na *Anthemis cotula e na Conyza Canadensis* se bem que a dimensão do aumento das diferentes características fosse altamente específico da espécie. A adição da serradura reduziu significativamente o aumento mediado do distúrbio em muitas das características investigadas. Apesar das diferenças na resposta das espécies alienígena invasoras às manipulações do solo, a adição de carbono pode ser usada como uma contra medida

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para combater efectivamente as invasões de certas plantas exóticas.

Key words: Alien invasive species, Kashmir Himalaya, sawdust, soil carbon addition, soil disturbance.

Introduction

Increased availability of resources, such as light, water, and soil nutrients, especially nitrogen, is known to promote alien plant invasions (Alpert & Maron 2000; Bleier & Jackson 2007). In fact, studies have shown that experimental application of nitrogen (Wedin & Tilman 1996), soil enrichment by nitrogen-fixing shrubs (Vitousek & Walker 1989), and aerial nitrogen deposition (Bobbink 1991), have increased the invasibility of habitats by alien plant species. Different methods have been proposed to reduce nutrient availability, for example, topsoil removal, maximizing off-take, and increasing storage in organic and inorganic nutrient pools (Eschen *et al.* 2006). The addition of carbon to the soil, accomplished through addition of sawdust, wood chips, activated-carbon, or sucrose has recently been proposed as a means to counter plant invasions, especially in habitats where nitrogen enrichment is taking place (Averett *et al.* 2004; Corbin & D'Antonio 2004).

Carbon enrichment induces soil microbial activity leading to increased immobilization of inorganic nitrogen (Blumenthal *et al.* 2003; Paschke *et al.* 2000; Perry *et al.* 2004). Several studies have demonstrated that carbon addition leads to decreased rates of net nitrogen mineralization (Averett *et al.* 2004), and nitrification (Gilliam *et al.* 2005), and reduced concentrations of ammonium (Hopkins 1998) and nitrate (Blumenthal *et al.* 2003) in the soil. Such alterations in resource availability have been shown to reduce the competitive ability of alien invasive plants (Perry *et al.* 2004; Reever Morghan & Seastedt 1999). The type of carbon source added to the soil, is likely to influence the soil environment and plant growth depending on the rate at which the carbon becomes available to microorganisms (Eschen *et al.* 2006). For example, a readily available carbon source, such as sucrose or pure carbon, may stimulate microbial activity within hours (Dalenberg & Jager 1981), while other sources, consisting of structurally more complex molecules, take longer to degrade (Magill & Aber 2000), especially when applied as coarse structures with small surface to volume ratios. The relatively short decay rate of sawdust makes it a potential substitute for the expensive sugar as a carbon source, while the addition of small pieces of wood may have a slower but longer-lasting effect on the soil environment and vegetation. In view of the relatively short decay rate, ease of application, and economic feasibility, most workers have used sawdust to manipulate soil nutrient availability (Wilson & Gerry 1995; Yarie & Van Cleve 1996).

Abandoned-arable soils are often characterized by high inorganic nitrogen levels, which lead to the rapid establishment of fast-growing annual and perennial invasive species. These species continue to dominate as long as the nutrient availability remains high, and thus impede the establishment of native plant species, even when such species are introduced by sowing (Kindscher & Tieszen 1998). Manipulation of nutrient availability is a potential means to facilitate native species establishment. Regardless of the source of carbon used, most previous studies have looked at differences between alien invasive species and native species in their response to experimental manipulation of soil nutrient availability (Lowe *et al.* 2002). However, differences among invasive species in their response to soil nutrient manipulations may be more important in understanding plant invasions. It is for this reason that the present study was conducted with the following objectives:

a. To investigate whether or not the growth and abundance of three phylogenetically related Kashmir Himalayan invasive species, *Anthemis cotula* L., *Conyza canadensis* Cronquist, and *Galinsoga parviflora* Cav., are promoted by soil disturbance;
b. To investigate whether carbon addition reduces the disturbance-affected growth and abundance of these invasive species; and
c. To see whether the interactive effect of soil disturbance and carbon addition is species- and trait-specific.

Materials and methods

The three phylogenetically related, herbaceous annual alien invasive species, namely *Anthemis* *cotula*, *Conyza canadensis*, and *Galinsoga parviflora*, belong to the family Asteraceae and are widely distributed in the Kashmir Himalaya, India (Khuroo *et al.* 2007). *Anthemis cotula* (stinking mayweed) is native to southern Europe to West Siberia (Erneberg 1999); *C. canadensis* (horse-weed) is native to North America (Noyes & Rieseberg 1999), and *G. parviflora* (gallant soldier) is native to tropical America (Canne 1977). *A. cotula* and *C. canadensis* are winter-annuals whereas *G. parviflora* is a summer-annual. The former two species behave as true ruderals by growing mostly in recently disturbed habitats, while *G. parviflora* grows in more competitive environments. The significant features of the plants, such as the lack of seed dormancy (in *C. canadensis* and *G. parviflora*), rapid growth and development, early flowering, many generations per growing season, and production of a great number of seeds in a wide range of environmental conditions, predispose these species to be trouble-some invaders (Rashid 2009).

Three study sites within the University of Kashmir (34° 5' to 34° 6' N latitude, 74° 8' to 74° 9' E longitude; altitude 1586 m above mean sea level) were selected for soil manipulation studies. These sites had varying abundances of *A. cotula*, *C. canadensis* and *G. parviflora.*

The field experiment was laid in a randomized block design and each treatment had 3 replicate plots of 2 × 2 m. No seeds or seedlings were added to the plots, in order to obtain natural plant densities. The treatments included: (a) soil disturbance (soil tillage), (b) soil disturbance + carbon addition (1.5 kg m^{-2} of sawdust incorporated into each 2 × 2 m tilled plots, following Alpert & Maron [2000]), and (c) control treatment (soil neither tilled nor carbon-enriched). A carbon addition only treatment was not included, because carbon addition, in the absence of tillage, would have been confounded with mulching. Tillage was performed in autumn (October 2006), when there was no vegetation in the field, to avoid the influence of seed rain from neighbouring species. Sawdust was incorporated into the soil up to a depth of about 10 cm, which marks the rooting zone of the three species, in order to avoid a mulching effect. Sawdust was obtained from local lumber mills and consisted mainly of *Populus* and *Salix* woods.

Five plants of each species from every treatment were randomly collected at maturity (August 2007) to assess the effect of the soil manipulation treatments on traits, such as plant height (cm), root, shoot and whole plant dry mass (g $plant^{-1}$) and numbers of capitula (per plant). Quadrats of 50 cm^2 were laid in the treated plots to record the density of each species. Root and shoot materials of the harvested replicate plant samples were weighed on an electronic monopan balance to compute dry mass, after oven drying at 80 °C to constant weight.

Trait means and their variances were computed using SPSS 10. Effect of each soil manipulation treatment on various traits of the three invasive species was statistically analysed through one-way ANOVA. Significant differences among the means were determined using Tukey's HSD test.

Results

Density was significantly increased in all the three species in response to soil disturbance (Fig. 1a), but the extent of increase varied between species. Compared to the control treatment, soil disturbance marginally increased density in *C. canadensis* and *G. parviflora* but greatly increased density in *A. cotula*. While carbon addition reduced density in *C. canadensis* and *G. parviflora*, compared with the controls, it did not do so in the case of *A. cotula.*

With respect to plant height, disturbance had the most significant positive effect in *C. canadensis,* though soil disturbance induced moderate increases in plant height in *A. cotula* and *G. parviflora* also (Fig. 1b). Carbon addition, on the other hand, had almost no effect on plant height in two of the three species compared with the disturbed plots, but reduced plant height in *C. canadensis* compared to both the disturbance treatment and the control.

Comparisons of the three species with respect to root, shoot and whole plant dry mass in relation to different experimental soil manipulations revealed that the most pronounced effect in all these attributes was recorded in *C. canandensis* in response to soil disturbance (Fig. 1c,d,e). *A. cotula* also showed an increase in shoot and whole plant dry mass (but not root biomass) as a response to soil disturbance. On the other hand, soil disturbance with carbon addition resulted in a reduction in shoot, root, and whole-plant biomass as compared to the control treatment in the case of *C. canadensis*, but not in the case of *A. cotula.* In the case of *G. parviflora,* although there was a statistically significant change in root, shoot and whole-plant biomass in response to the experimental treatments, this constituted only a marginal change over the values of these variables in the control treatment.

While the number of capitula in all the three species increased in response to soil disturbance the greatest increase was registered in *C. cana-*

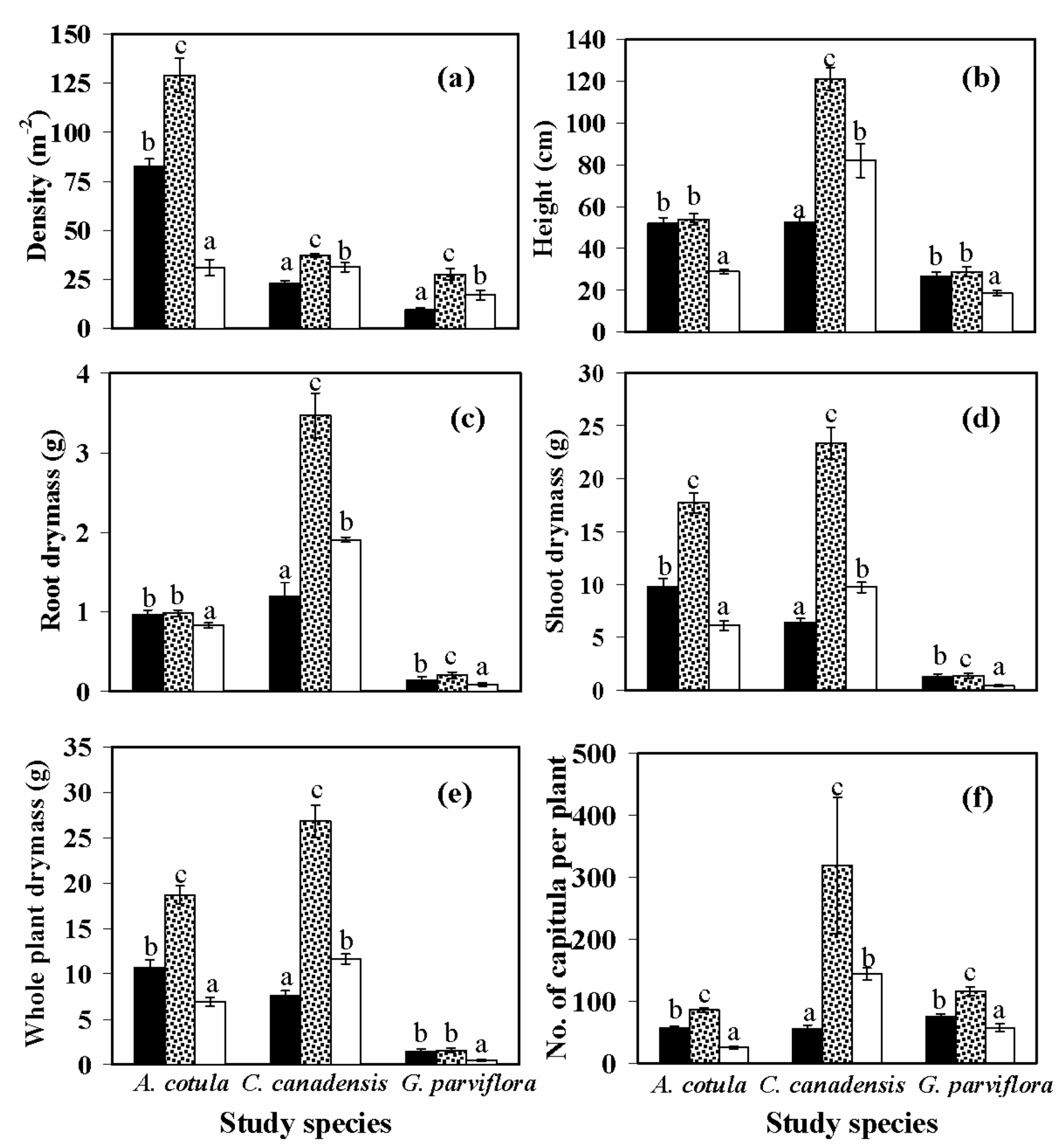

Fig. 1. Response (mean ± SE) of three alien invasive species (*A. cotula, C. canadensis* and *G. parviflora*) to different treatments viz., disturbed soils with (black bars) and without (stippled bars) carbon addition, and undisturbed soils without carbon addition (white bars). Different letters indicate significant differences among treatments within species.

densis (Fig. 1f). However, reduction in number of capitula due to carbon addition was also highest in this species. Such large variations in the number of capitula per plant in response to the different treatments were not observed in *A. cotula* and *G. parviflora.*

Discussion

Differences amongst the three invasive species

Increase in plant density in response to soil disturbance that we observed is supported by other observational (see D'Antonio *et al.* 1999 for a comprehensive review) and experimental studies (e.g., Burke & Grime 1996; Hobbs & Atkins 1988; Leishman & Thomson 2005). The increased density could be due to alteration of resource availability, either because of destruction of resident species or by the direct increase in resource supply (Davis *et al.* 2000; Levine *et al.* 2003). In addition to increased resource availability, interaction of disturbance with other factors could also favour alien invasive species during recruitment and establishment. For example, germination and seedling growth, two critical stages in the successful colonization of invasive plant species, have, in many cases, been found to be dependent on gap size (D'Antonio 1993; Hobbs 1991; King & Grace 2000) or disturbance-mediated environmental cues such as light and soil nutrients, as in *A. cotula* (Rashid *et al.* 2007).

Notwithstanding inter-specific differences, significant increases in many of the studied traits in the three species in response to soil disturbance attest to its stimulatory influence on growth, and presumably, species invasiveness. *A. cotula* and *C. canadensis*, being ruderals, appear to take advantage of greater resource availability on account of removal of native vegetation and increased or fluctuating resource supply, while *G. parviflora,* being a competitive species, does not appear to benefit as much from disturbance.

While differences between native and exotic species traits to disturbance have been widely demonstrated (Alpert & Maron 2000; Bleier & Jackson 2007; Larson 2003; Leishman & Thomson 2005), the present study clearly establishes that differences can occur among different exotic invasive species, as well. Thus, it is difficult to generalize control measures to combat alien plant invasions. For example, carbon addition may serve as a practical countermeasure to invasion by fast growing, non-mycorrhizal alien species, but may fail to control slow growing mycorrhizal species. Therefore, species-specific studies to control alien plant invasions are required. Crucial information in this regard is lacking for many species and the challenge for the invasion ecology community is to collate such information and to make it widely available (Pysek & Richardson 2007).

Management implications

Soil disturbance promotes growth and abundance of plant species, mainly by increasing the availability of a limiting resource, such as nitrogen (King & Buckney 2002). Microbial immobilization of nitrogen, encouraged by addition of carbon, could be expected to reduce the density and growth of plant species. This would account for differences in plant density observed between sawdust-treated and untreated plots (Fig. 1a).

The present study of sawdust incorporation into soil significantly reduced the disturbance-induced increase in various traits. Similar results have been reported by Wilson & Gerry (1995), Reever Morghan & Seastedt (1999), Alpert & Maron (2000), Cione *et al.* (2002) and Blumenthal *et al.* (2003). In addition to its general effect of reduced growth (Blumenthal *et al.* 2003), carbon addition also affects the growth of plant species in a species-specific way and such results are supported by studies of Eschen *et al.* (2006). Thus restoration efforts attempting to reduce alien invasive species by reducing nitrogen availability would need to take into account the differential responses of these species to nitrogen. Despite the differences in response of individual alien invasive species to various soil manipulations, we suggest that soil carbon addition should be blended with other measures in order to effectively manage alien plant invasions. It is unlikely that any single management tool will be completely effective in restoring native plant communities because exotic and native species use many different mechanisms to succeed. Further research is needed (1) to study the effect of different concentrations of sawdust on native and alien species, (2) to study the long-term effects of sawdust amendments, and (3) to test soil nitrogen mineralization across the experimental treatments.

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