Biol Invasions
DOI 10.1007/s10530-007-9151-8

ORIGINAL PAPER

Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile

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Received: 18 July 2007 / Accepted: 26 July 2007

Abstract Invasive species can increase fire frequency and intensity, generating favorable conditions for their self-perpetuation. Mediterranean south-central Chile may be especially prone to the effects of invasive species on fire regimes because it is less adapted to fire and it contains a highly endemic flora. *Teline monspessulana* (L.) K. Koch (syn. *Cytisus monspessulanus* L.; *Genista monspessulana* (L.) L.A.S. Johnson) is an introduced shrub that forms monotypic stands or is present as an understory species in native forests as well as in forestry plantations. Dense *T. monspessulana* stands are completely destroyed by fire, generating the conditions for it seeds to germinate and establish an abundant regeneration, with up to 900 plants/m^2. We report key evidence on abundance and biomass in adult stands, and patterns of seed bank and regeneration after fire in stands of *T. monspessulana* around the city of Concepción, Chile. We estimated living biomass in pure stands and underneath *Eucalyptus* plantations. In burned areas, we assessed *T. monspessulana* seed bank and studied regeneration patterns. We found that *T. monspessulana* densities reaches 52,778 plants/ha and 8.92 ton/ha in pure stands and 34,223 plants/ha and 2.31 ton/ha underneath *Eucalyptus* plantations. *T. monspessulana* generates small caliper fuel and acts as a ladder-fuel. Large soil seed banks allow for abundant regeneration after fire, with mean densities of 877,111 plants/ha, but an overall mortality of 37.2% in the first year after the fire. The high values of regeneration compared to final densities in adult stands suggest that density-dependent mortality. Our results indicate that *T. monspessulana* regeneration is not only favored by fires, but also that the species creates favorable conditions for intense and continuous fires, both under pure conditions, but also associated to exotic tree plantations. To understand the implications of positive feedbacks between invaders and fire, we recommend focusing in the mechanisms by which they increases fuel accumulation and fuel flammability, and how higher fire frequency and intensity favors invasive species recruitment over native species. Comprehension of this dynamics will allow for better management and control of these invasions which have major ecological, economical and social implications.

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Keywords Invasive species · Wildfires fuel · Impacts · Seedbank · Post-fire shrub regeneration

Introduction

Invasive species can increase fire frequency and intensity, generating favorable conditions for their self-perpetuation (D'Antonio and Vitousek 1992; Mack and D'Antonio 1998; D'Antonio 2000; Brooks et al. 2004). Invasive plants may increase fuel load or alter other fuel attributes such as flammability and continuity (Brooks et al. 2004). Additionally, they may be better adapted than their native counterparts to regenerate after fire, either by seeds or resprouting, enabling a fast recolonization or invasion of burned areas (Radford et al. 2001). The positive feedback between invasive species and fire is a major cause of unidirectional change in invaded ecosystems, especially in ecosystem that have not evolved in the presence of frequent and intense fire regimes (Brooks et al. 2004). The positive feedback between invasive species and fire can have major community and ecosystem effects, changing local community dynamics, altering biodiversity and generating long-lasting consequences on biogeochemical cycles (Mack and D'Antonio 1998; Keeley 2002; Grigulis et al. 2005).

In Mediterranean-type ecosystems the impact of invasions on fire regimes could have important consequences because fire plays an important role in the dynamics of plant communities, plant evolution, and landscape structure (Trabaud 1991; Montenegro et al. 2004). Nevertheless, when the natural fire regime is modified by human activities, even highly fire-adapted communities could increase their invasibility and change their long-term composition (Keeley 2002). For example, in the South African fynbos native species have reproductive adaptations to fire (Holmes and Cowling 1997). In spite of this, fire seems to favor the invasion of fynbos by other Mediterranean alien plants, such as *Acacia*, *Hakea* and *Banksia* species introduced from Australia (Richardson et al. 1987; Holmes and Cowling 1997) or by *Pinus* from Europe and North America (Richardson and Brown 1986; Richardson 1988).

Mediterranean south-central Chile may be especially prone to the effects of invasive species on fire regimes. Historically, fire occurred at a much lower frequency than other Mediterranean areas (Arroyo et al. 1995). Therefore, increases in fire frequency and intensity may be more influential for the less fire-adapted native species. The area is currently impacted by intensive agriculture and exotic *Pinus* and *Eucalyptus* plantations, which have increased the rate of anthropogenic fires. In addition, an exponential increase in urban and highway development has caused the expansion of numerous invasive species some of them with potential to modify fire regimes (Arroyo et al. 2000; Pauchard and Alaback 2004). While Central Chile has approximately 2,500 native species, over 700 non-native naturalized species have been documented in this region (Arroyo et al. 2000; Matthei 1995). Plant invasions are especially troublesome considering the high level of endemism (Arroyo et al. 2000; Pauchard et al. 2004; Figueroa et al. 2004).

One of the most widely distributed invasive species of the Fabaceae family in central Chile is *Teline monspessulana* (L.) K. Koch (syn. *Cytisus monspessulanus* L.; *Genista monspessulana* (L.) L.A.S. Johnson). *T. monspessulana* is an introduced shrub from Europe that forms monotypic stands or is present as an understory species in native forests as well as in forestry plantations. Originally from the Mediterranean Basin, and invasive in several regions of the world (e.g. Johnson 1982; Adams and Simmons 1991; Bossard 2000; Alexander and D'Antonio 2003), the species can now be found from the Valparaiso Region to the Lake region in Chile, both in the understory of degraded forests and in heavily disturbed areas where it outcompetes most native species (Matthei 1995). This plant is a nitrogen fixer, which is able to colonize highly disturbed mineral soils. *T. monspessulana* seeds are covered with a hard cuticle which allows the seed to maintain its viability for years. This condition allows for the accumulation of large seedbanks containing over 10,000 seeds/m^2 (Alexander and D'Antonio 2003 in California), an attribute that has been reported for invasive Fabaceae shrubs worldwide (Bossard 1991, 2000; Holmes and Cowling 1997; Alexander and D'Antonio 2003).

Dense *T. monspessulana* stands are completely destroyed by fire, generating the conditions for it seeds to germinate and establish an abundant regeneration, with up to 900 plants/m^2 (Fig. 1, García et al. 2007). Its abundant presence in seed banks and fast growth following fire or other heavy disturbances causes *T. monspessulana* to be considered as a highly aggressive weed (Matthei 1995). Additionally, this species may increase fuel load and flammability, thus increasing frequency and intensity of fire regimes. However, the direct and indirect effects of these invasions have not been explicitly measured. Thus, the aim of this paper is to provide evidence of a possible positive feedback between plant invasions and fire, specifically on the role of *Teline monspessulana*. We report key evidence on abundance and biomass in adult stands, and patterns of seed bank and regeneration after fire in stands of *T. monspessulana* around the city of Concepción, Chile. This southern hemisphere example of positive feedback between fire and plant invasions adds new evidence to this globally known phenomenon.

Methods

Study area

The study area was located in the Coastal Range around the city of Concepción (36°50,296′ S, 73°02,866′ W) between 30 and 175 m.a.s.l. Climate is transitional between Mediterranean and temperate with a 4-month dry season during summer and 1.100 mm of annual precipitation. Average annual temperature is 12°C. Soils are well-developed granitic clay. Land use is dominated by exotic tree plantations (*Pinus radiata*, *Eucalyptus* spp and *Acacia melanoxylon*) and small fragments of mixed evergreen and deciduous native forests (Pauchard et al. 2006). We studied three conditions where *T. monspessulana* is a dominant species: (1) adult pure stands of *T. monspessulana (6 years old)*, (2) adult stands of *T. monspessulana* underneath an adult *Eucalyptus* plantation and (3) an area of exotic tree forests affected by fire in February of 2005. The burned condition was stratified in three units based on remaining tree cover: low, medium and high.

Field data and analyses

Adult stands

We sampled the abundance of *T. monspessulana* using 1 m^2 circular plots. A total of 45 plots were randomly distributed in each condition. Height of each *T. monspesulanna* plant was recorded in 10 cm height classes in each plot. We estimated living biomass in pure stands and underneath *Eucalyptus* plantations using biomass functions based on height and collar diameter (CD). Linear functions

Fig. 1 *Teline monspessulana* interaction with fire. (**A**) Monotypic adult stand, (**B**) Post-fire condition, (**C**) Regeneration two months after fire (April), (**D**) Regeneration in mid-spring (October)

(Biomass = $a + b * CD^2H^2$) were adjusted using 40 individuals in each stand condition (Mean $R^2 = 0.837$). Dry biomass was registered after 48 h at 80°C. Total biomass for each 1 m^2 plot was then calculated by summing the estimated biomass, based on the biomass adjusted function, of each recorded individual.

Post-fire stands

We collected 6.5 cm deep soil cores (diameter = 5 cm) to assess seed bank in the area that was affected by fire. Nine samples were collected for each cover unit ($n = 27$). Based on a preliminary sample which found no significant differences in seed bank among depths, we compare the complete sample with no stratification by depth.

Teline monspessulana regeneration in the burned area was estimated using the same methodology as described for adult stands, with 15 plots per each canopy cover unit. Regeneration, in these plots, was monitored from early spring 2005 (September) to mid fall 2006 (May). Detailed results of the monitoring protocol are presented in García et al. (2007).

We used ANOVA and pair-wise comparisons (Tukey test) in SPSS 14.0 to compare *T. monspessulanna* variables across conditions (e.g. total abundance, seedling abundance, and total biomass).

Results and discussion

Adult stands

In adult stages, *T. monspessulana* densities reach 52,778 plants/ha in pure stands and 34,223 plants/ha underneath *Eucalyptus* plantations (Tukey test, $P < 0.01$, Fig. 2). We found extremely low values for density of regeneration in pure stands (444 ± 310 plants/ha; Mean ± SE) and slightly, but not significantly, higher values underneath Eucalyptus plantations (4,889 ± 1215 plants/ha; Mean ± SE) (Tukey test, $P > 0.01$, Fig. 2).

We found a mean live biomass in pure stands of *T. monspessulana* of 8.92 (±0.40) ton/ha, and underneath *Eucalyptus* an average of 2.31 (±0.14) ton/ha. Differences in total living biomass between the two conditions are explained both by higher density and

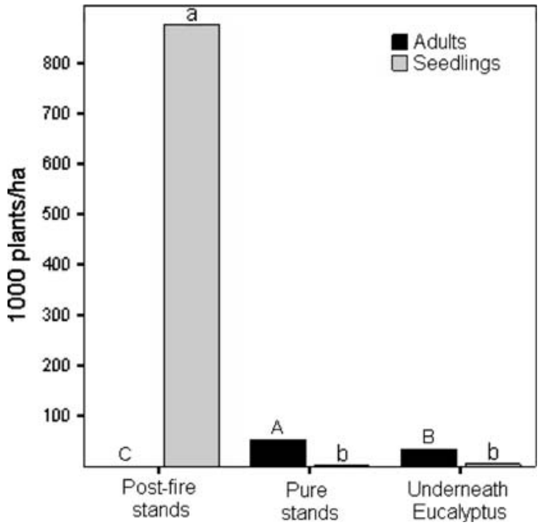

Fig. 2 Total number of individuals of *Teline monspessulana* (adults >1 m; seedlings <1 m) in post fire stands, pure stands and stands underneath *Eucalyptus* plantations. Letters indicate significant differences (Tukey test, $P < 0.01$)

higher individual size in pure stands. Increased fuel loads caused by *T. monspessulana*, can increase fire intensity but the species can also act as a ladder-fuel, increasing the probability of crown fires reaching an average height of the tallest 20% of 2.80 m in pure stand and 2.39 m underneath *Eucalyptus* plantations. The addition of ladder fuels increases vertical fuel continuity, allowing fires to travel from the surface into the crowns of shrubs and trees. This may not affect the frequency of fires, but it can affect their intensity and perhaps their spatial extent (Brooks et al. 2004). Additionally, *T. monspessulana* provides large amounts of small caliper fuels in pure stands (Collar diameter = 1.22 ± 0.02) and underneath plantation (CD = 0.82 ± 0.02), which are more prone to burn even in less favorable fire conditions.

Post-fire stands

We found a high variability on the seed bank in burned areas. In areas with higher tree cover, seed bank was 1.121 seeds/m^2 (±303). In areas with intermediate cover, seedbank was 510 seeds/m^2 (± 241). Finally, for the more open environments, average seed bank was 3.975 (±1636) seeds/m^2. Seed viability in seed banks of *T. monspessulana* has been reported to reach up to 100% (Paynter et al. 1998;

Funke 1999; Miranda 2003; González 2007), but with low germinative capacity (ca. 2–13%) (Funke 1999; Miranda 2003; González 2007). However, exposition to temperatures between 90 and 108,5°C increases considerable the germinative capacity reaching 32% in laboratory conditions (Funke 1999; Gonzales 2007). Our data suggest that the ratio between total regeneration and seedbank is approximately 17.4% when estimated as the mean ratio for the 1 m^2 plots.

The recorded seed bank appears to be sufficient to produce really high levels of *T. monspessulana* seedlings for recolonization after severe fire events. These densities are within ranges of those reported for the County of Marin (California) with 900–10.582 semillas m^{-2} (Alexander and D'Antonio 2003). A review by Bossard (2000) reports seed bank densities for *T. monspessulana* range from 465–6,733 seeds/m^2. While seed bank densities of 3,774 seeds/m^2 and 2,563 seeds/m^2 were recorded at two sites in Australia (Adams and Simmons 1991). Seed bank is definitively not a constraint for this species, even if the most superficial portion of it can be damaged by intense fires. Thus, fire appears to be an important estimulador of germination, increasing germinative capacity, a situation that has been described extensively for other Fabaceae species (Tarrega et al. 1992; Mucunguzi and OryemOriga 1996; Herranz et al. 1998; Tozer 1998; Morrison and Renwick 2000; Radford et al. 2001; Auld and Denham 2006; Kulkarni et al. 2007).

In areas affected by fires, regeneration is logarithmically higher than in adult stands (Tukey test, $P < 0.01$), suggesting limited recruitment after adult plants close their canopies or there is competition for light with tree canopy cover. Mean regeneration after fire reached the 877,111 (±299,086) plants/ha, but an overall mortality of 37.2% in the first year after the fire. The high values of regeneration compared to final densities in adult stands suggest that density-dependent mortality associated with competition for resources in thick monotypic stands.

Conclusions: disentangling the interactions between fire and invasive species

Our results indicate that *T. monspessulana* regeneration is not only favored by fires, but also that the species creates favorable conditions for intense and continuous fires, both under pure conditions, but also associated to exotic tree plantations. This behavior has been reported for a number of invasive species that maintain their densities in the long term by increasing the rate and intensity of fire regimes (Mack and D'Antonio 1998; Brooks et al. 2004). As Brooks et al. (2004) propose, increases in fire frequency and intensity, and the consequent impact on the ecosystem is determined by the increase in fuel load, fuel flammability and extension of the affected area. Additionally, some invaders may change fuel to finer fuel and, thus, increase vertical and horizontal continuity, allowing fire to reach into the tree canopy, which has been shown here for *T. monspessulana*. All these factors combined results in a more flammable vegetation and fire with unpredictable behavior, increasing the magnitude of damage and decreasing forest fire control. The positive feedback is perpetuated when after a fire; invasive species increase their competitive advantage over native species, which are less adapted to intense and frequent fires.

To understand the implications of this relationship between fire and *T. monspesulanna* or other fire-promoting invasive species, we recommend focusing on four main questions:

(1) At the landscape scale, is there a positive correlation between fire frequency and the abundance of the fire-promoting invasive species?
(2) Which are the main differences in fuel characteristics between native vegetation or other dominant land-uses and the invasive species stands?
(3) How different in the short-term respond of native species compared to that of the invasive species to fire disturbances?
(4) Which are the long-lasting effects on native biota and ecosystem functions of increasing fire frequency and intensity associated to the invasive species?

Research should focus in understanding the mechanisms by which some invasive species increases fuel accumulation and fuel flammability, creating conditions that may change fire regimes by increasing fire frequency and intensity. Additionally, it should be explored how higher fire frequency and intensity favors invasive species recruitment over native species, favoring the replacement of native species by the invader and creating novel communities dominated by non-native species. Studies about these ecosystem changes would benefit from the use of a comprehensive multiscale approach, enabling integration across scales (Pauchard and Shea 2006).

Invasive species that are able to modify disturbance regimes can have a much higher impact on native biota. Therefore, studies on the processes and mechanism of positive feedbacks between plant invasion and fire regimes should be a priority, especially in areas where there has only recently been an awareness of the effects of plant invasions. Comprehension of this dynamics will allow for better management and control of these invasions which have major ecological, economical and social implications.

Acknowledgements To Jorge Cancino for his help with biomass models. To Macarena González for her collaboration in the seed-germination studies. This study was funded by Fondecyt grant #1070488, and grant ICM 05-002.

References

Adams R, Simmons D (1991) The invasive potential of *Genista monspessulana* (Montpellier broom) in dry sclerophyll forest in Victoria. Vic Nat 108(4):84–89

Alexander J, D'Antonio CM (2003) Seed bank dynamics of French broom in coastal California grasslands: effects of stand age and prescribed burning on control and restoration. Restor Ecol 11(2):185–197

Arroyo MTK, Cavieres L, Peñaloza A, Riveros M, Faggi A (1995) Relaciones fitogeográficas y patrones regionales de riqueza de especies en la flora del bosque lluvioso templado de Sudamérica. In: Armesto J, Villagrán C, Arroyo MTK (eds) Ecología de los Bosques Nativos de Chile, Editorial Universitaria, Santiago, Chile, pp 71–100

Arroyo MTK, Marticorena C, Matthei O, Cavieres L (2000) Plant invasions in Chile: present patterns and future predictions. In: Mooney HA, Hobbs RJ (eds) Invasive species in a changing world. Island Press, Covelo, California, pp 385–421

Auld TD, Denham AJ (2006) How much seed remains in the soil after a fire? Plant Ecol 187(1):15–24

Bossard CC (1991) The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. Am Midland Nat 126:1–13

Bossard CC (2000) *Genista monspessulana* (L.) L. Johnson. In: Bossard CC, Randall JM, Hoshovsky MC (eds) Invasive plants of California's wildlands. University of California Press, California, pp 203–208

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, Di Tomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. BioScience 54(7):677–688

D'Antonio CM (2000) Fire, plant invasions, and global changes. In: Mooney HA, Hobbs RJ (eds) Invasive species in a changing world. Ireland Press, Covelo, California, pp 65–95

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Figueroa JA, Castro SA, Marquet PA, Jacksic FM (2004) Exotic plants invasions to the mediterranean región of Chile: causes, history and impacts. Rev Chil Hist Nat 77:465–483

Funke C (1999) Efecto de la temperatura en la germinación de semillas de Retamilla (*Teline monspessulana* (L.) K. Koch), un estudio de laboratorio. Undergade tesis, Facultad de Ciencias Forestales, Universidad de Concepción, Chile, 39 pp

García RA, Pauchard A, Peña E (2007) Banco de semillas, regeneración y crecimiento de *Teline monspessulana* (L.) K. Koch después de un incendio forestal. Gayana Bot XX:XX–XX

González M (2007) Efecto del fuego en la germinación de de cuatro especies introducidas en la zona centro sur de Chile. Undergade tesis, Facultad de Ciencias Forestales, Universidad de Concepción, Chile, 38 pp

Grigulis K, Lavorel S, Davies ID, Dossantos A, Lloret F, Vilà M (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, *Ampelodesmos mauritanica* in Catalan shrublands. Global Change Biol 11(7):1042–1053

Herranz J, Ferrandis P, Martínez-Sánchez J (1998) Influence of heat on seed germination of seven Mediterranean *Leguminosae* species. Plant Ecol 136:95–103

Holmes PM, Cowling RM (1997) Diversity, composition and guild structure relationships between soil-stored seed banks and mature vegetation in alien plant-invaded South African fynbos shrublands. Plant Ecol 133:107–122

Johnson PN (1982) Naturalised plants in south-west South Island, New Zealand. New Zealand J Bot 20:131–144

Keeley JE (2002) Fire and invasives in Mediterranean-climate ecosystems of California. In: Wilson TP, Galley KEM (eds) Proceedings of the invasive species workshop. The role of fire in the control and spread of invasive species. Tall Timbers Research Station, Tallahassee, Florida, pp 81–94

Kulkarni MG, Sparg SG, Van Staden J (2007) Germination and post-germination response of Acacia seeds to smoke-water and butenolide, a smoke-derived compound. J Arid Environ 69(1):177–187

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trenes Ecol Evol 13(5):195–198

Matthei O (1995) Manual de malezas que crecen en Chile. Alfabeta Impresores, Santiago, Chile, 549 pp

Miranda V (2003) Caracterización del banco edáfico de *Teline monspessulana* (L.) K. Koch en tres sitios de la provincia de Concepción. Undergade tesis, Facultad de Ciencias Forestales, Universidad de Concepción, Chile, 39 pp

Montenegro G, Ginocchio R, Segura A, Keely JE, Gómez M (2004) Fire regimes and vegetation responses in two

Mediterranean-climate regions. Rev Chil Hist Nat 77:455–464

Morrison DA, Renwick JA (2000) Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region. Aust J Bot 48(1):71–79

Mucunguzi P, OryemOriga H (1996) Effects of heat and fire on the germination of *Acacia sieberiana* DC and *Acacia gerrardii* Benth in Uganda. J Tropical Ecol 12:1–10

Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. Conserv Biol 18:238–248

Pauchard A, Aguayo M, Peña E, Urrutia R (2006) Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepción, Chile). Biol Conserv 127:272–281

Pauchard A, Cavieres L, Bustamante R, Becerra P, Rapoport E (2004) Increasing the understanding of plant invasions in southern South America: first symposium on Alien Plant Invasions in Chile. Biol Inva 6:255–257

Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biol Inva 8:399–413

Paynter Q, Fowler S, Memmott J, Sheppard A (1998) Factors affecting the establishment of *Cytisus scoparius* in southern France: implications for managing both native and exotic populations. J Applied Ecol 35(4):582–595

Radford IJ, Nicholas DM, Brown JR (2001) Impact of prescribed burning on *Acacia nilotica* seed banks and seedlings in the Astrebla grasslands of northern Australia. J Arid Environ 49(4):795–807

Richardson DM (1988) Age structure and regeneration after fire in a self-sown *Pinus halepensis* forest on the Cape peninsula, South Africa. South Afr J Bot 54:140–144

Richardson DM, Brown PJ (1986) Invasion of mesic mountain fynbos by *Pinus radiata*. South Afr J Bot 52:529–536

Richardson DM, Van Wilgen BW, Mitchell DT (1987) Aspects of the reproductive ecology of four Australian *Hakea* species (Proteaceae) in South Africa. Oecologia 71:345–354

Tarrega R, Calvo L, Trabaud L (1992) Effect of high temperatures on seed germination of two woody Leguminosae. Vegetation 102(2):139–147

Tozer MG (1998) Distribution of the soil seedbank and influence of fire on seedling emergence in *Acacia saligna* growing on the central coast of New South Wales. Austr J Bot 46(5–6):743–755

Trabaud L (1991) Is fire an agent favouring plant invasion? In: Groves RH, di Castri F (eds) Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge, UK, pp 179–190