

Impact of the invasive plant *Syzygium jambos* (Myrtaceae) on patterns of understory seedling abundance in a Tropical Premontane Forest, Costa Rica

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Received 25-VII-2005. Corrected 12-I-2006. Accepted 22-III-2006.

Abstract. Habitat fragmentation, along with other human-induced disturbances, increase the vulnerability of native habitats to be invaded by aggressive, ecologically released, exotic species. *Syzygium jambos* (L.) Alston (Myrtaceae, Rose Apple) is an important invader still spreading throughout Hawaii, the Antilles, Central and South America. This study examines the effects of *S. jambos* on plant understory diversity in a 25 ha Tropical Premontane Moist Forest in Atenas, Alajuela, Costa Rica, a protected watershed that supplies drinking water for several human communities. Our final objective is to develop a management strategy combining water protection with the preservation of a representative sample of the original plant diversity in the area. Thirty 2 X 2 m plots were distributed throughout the Municipal Forest maintaining a minimum of 10 m between plots, and 2 m from trails, to sample all understory seedlings and saplings of *S. jambos*, *Coffea arabica* (coffee) and tree seedlings. We found a clear dominance of *S. jambos* over all other understory plants. Of the total 1 285 sampled plants, *S. jambos* comprised 51%, coffee seedlings represented 14.78%, being the rest tree seedlings. *Syzygium jambos* had the highest density (5.46 plants/m², S.D. = 6.44) compared to tree (3.67 plants/m², S.D. = 3.44) and coffee seedlings (1.58 plants/m², S.D. = 2.13). There was a highly significant negative relationship between the relative abundance of *S. jambos* and tree ($r^2 = 0.52$, $p < 0.00001$) and coffee seedlings ($r^2 = 0.28$, $p < 0.002$). The abundance of coffee seedlings did not affect the abundance of tree seedlings ($r^2 = 0.01$, $p < 0.58$). Since the canopy of the Municipal Forest is relatively closed and composed of a monolayer of trees with almost no overlapping crowns, we found no relationship between canopy cover and the abundance of *S. jambos*. The height distribution indicated that the majority of *S. jambos* individuals were seedlings and saplings (height ≤ 1.5 m), with only 4.6% classified as adults, (height ≥ 2 m). The results show a clear role of *S. jambos* as an aggressive, invasive species within the Municipal Forest. This invasion is enhanced by both the ecological characteristics of the species and the fragmentation of the forest by coffee farming around the site. Among a variety of management possibilities, an ecosystem-level approach of manually removing *S. jambos* over time while replanting native species appears to be the preferred strategy, given the intended continued use of the Municipal Forest as a source of drinking water and as a representative sample of the original vegetation of the area. Rev. Biol. Trop. 54(2): 415-421. Epub 2006 Jun 01.

Key words: *Syzygium jambos*, invasive species, forest management, water quality management, Costa Rica.

The spread of invasive, exotic plant species, especially when coupled with widespread habitat alteration, continues to be the major threat to global biodiversity (Soule

1990, D'Antonio and Vitousek 1992, Goodwin *et al.* 1999). Invasive plants are endowed with suites of ecological traits that allow them to spread rapidly, infiltrate alien ecosystems,

and out-compete native plants, taking over their niches and often removing those native species from the ecosystem altogether. These traits include a short juvenile period, early and almost continuous, profuse reproduction, widely dispersed seeds, high initial germination, fast growth rate of seedlings, shade tolerance, and capacity to self-pollinate (i.e., *Miconia calvescens*, Meyer and Florence 1996, Rejmanek and Richardson 1996). Many of the best invaders are “r-strategists” because the majority of invasions take place in human-disturbed areas (Baker 1974, Rejmanek *et al.* 1996).

Syzygium jambos (L.) Alston (Myrtaceae, Rose Apple) is a small tree (10–15 m) native to Southeast Asia that has been introduced into the Hawaiian Archipelago, Southern Florida and the Neotropics due to its importance as a shade tree, edible fruits and showy flowers (Amshoff 1958). It has become an aggressive invader species in Puerto Rico, the Dominican Republic, and Hawaii, where it dominates forest stands, impoverishing the native flora and increasing the risk of extinction of endangered taxa. It represents one of the 40 most aggressive invasive angiosperms listed by Rejmanek and Richardson (1996).

In Costa Rica, *S. jambos* is traditionally used as a living fence and, less frequently, as a shade tree for coffee plantations. It is pollinated by bees (Lughadha and Proenca 1996) and dispersed by a wide variety of birds and bats. *S. jambos* produces abundant fruits with polyembryonic seeds (1 cm in diameter), and shade tolerant, flexible seedlings able to resist mechanical damage (Di Stefano *et al.* 1998). In addition, it has a high tannin concentration, being highly defended against herbivores (Di Stefano *et al.* 1998). These conditions have facilitated the colonization of disturbed forests adjacent to coffee plantations in the Central Valley of Costa Rica (Di Stefano *et al.* 1998) where it potentially outcompetes slow-growing tree seedlings for light, nutrients, and space. Following an infiltration pattern of invasion (Wilson and Lee 1989), *S. jambos* has found favorable conditions in disturbed forests, such

as lack of predators and pathogens during the first stages of regeneration, and appropriate conditions for germination and seedling establishment. The small, fragmented forests still surviving in the Central Valley are drained of native tree species due to higher rates of local extinction and recruitment limitation (lack of enough reproductive adults and seeds failing to arrive to safe sites) and are prone to being dominated by exotic, invader species. In this study, we analyze the impact of *S. jambos* on patterns of understory seedling diversity and density at the Municipal Forest of Atenas (Alajuela, Costa Rica), a 25 ha forest fragment surrounded by coffee plantations, and discuss alternatives for the management of this invader species.

MATERIAL AND METHODS

Study Site. The study was done at the Municipal Forest of Atenas, Alajuela, Costa Rica (9°58'21" N, 84°26'24" W) in October 2003. This 25 ha tropical premontane moist forest fragment (1 013 m in elevation) benefits from permanent protection due to its importance as a source of potable water for neighboring communities. The topography of the forest is diverse, ranging from flat terrain to steep areas of 45° slopes. The Municipal Forest is a late successional forest of about 40 years of regeneration. The forest is connected to other small forest patches only along 7.8% of its perimeter, whereas shaded coffee plantations line 56.5% of its border; the rest is bordered by Highway 3. Canopy height is close to 25 m, and two well-defined strata can be distinguished. The forest maintains 119 tree species distributed into 51 families (Brassil *et al.* 2000), but it is dominated by secondary successional species such as *Anacardium excelsum*, *Luhea semannii*, *Ceiba pentandra*, *Zanthoxylum* sp., and *Bravaisia intergerrima*. In addition to abundant *S. jambos* seedlings, we observed an infiltration of coffee seedlings coming from nearby plantations.

Density of *S. jambos*. To measure the density of *S. jambos*, we used 30 plots of 2 X 2 m distributed throughout the Municipal Forest following the outline of the trails. Plots were separated by at least 10 m and were located at least 2 m from the edge of the trail. Within each plot, we measured the number and height of all *S. jambos* plants and recorded the diameter at breast height (DBH, 1.3 m) in individuals ≥ 2 m. In addition, we located all seedlings and saplings from other species within the plots and recorded their number. The percentage of canopy cover above the plot was measured with a spherical densiometer model C (Forestry Suppliers) held in the middle of the plot and pointing south.

Population structure of *S. jambos*. Histograms were inspected to determine the distribution of *S. jambos* in different size classes. If height distribution is concentrated on small size classes (i.e., plants ≤ 1.5 m), it could be that *S. jambos* has the ability to germinate and survive in the shade but is suppressed to move to higher size classes by low light conditions. To determine this, we related the abundance of different size classes with the percentage of canopy cover. We expected seedling and sapling height to increase with increasing canopy aperture.

Impact of *S. jambos* on understory diversity. We used linear regression analyses to test the significance of the relationship between the relative abundance of *S. jambos* per plot and the relative density of other tree seedlings, as well as the significance of the relationship between *S. jambos* and coffee seedling and sapling relative abundance. If *S. jambos* is taking over the space in each plot, we will observe a negative relationship (high density of *S. jambos* vs. low density of tree and coffee seedlings). The relative abundance of seedlings from tree species was transformed following the Box and Cox transformation (Draper and Smith 1981) to control the heterogeneity of variance with increasing sample size as reflected in an initially atypical residual pattern. The relative

abundance of coffee seedlings was transformed using the square root transformation to fit the normal distribution (Shapiro-Wilk test = 0.94, $p = 0.1$). In addition, we explored the potential of coffee plants to become invaders by looking at the relationship between relative abundance of coffee seedlings per plot vs. the abundance of tree seedlings (excluding *S. jambos*). Probability values for these regressions were adjusted using the Bonferroni correction following Rice (1988). All analyses were done using the JMP IN statistical software version 4.0.4 (Sall *et al.* 2001).

RESULTS

Impact of *S. jambos* on understory diversity. Of the total 1 285 sampled plants, *S. jambos* made up 51%, coffee seedlings represented 14.78% and the rest was made of tree seedlings. Thus, it was not strange to observe a relatively high density (5.46 plants/m², S.D. = 6.44) of *S. jambos* throughout the sampled area (120 m²), which was higher than the average density of tree (3.67 plants/ m², S.D. = 3.44) and coffee seedlings (1.58 plants/ m², S.D. = 2.13). The high values of standard deviation reflect negative interactions between the abundance of *S. jambos* and that of coffee and tree seedlings since plots that were dominated by *S. jambos* had few seedlings from the other two. Congruent with this, we found a significant negative relationship between the relative abundance of *S. jambos* and tree (Fig. 1a) and coffee seedlings (Fig. 1b). However, the abundance of coffee seedlings did not affect the abundance of tree seedlings (Fig. 1c).

Influence of light conditions. Levels of canopy aperture varied between 55-92% with an average of 73.76% (S.D. = 10.25%). The canopy at the Municipal Forest is relatively closed and composed of a monolayer of canopy trees with almost no overlapping crowns. We did not find large gaps of significant importance (i.e., above 30 m²). Shade conditions were prevalent throughout most of the study site. Accordingly,

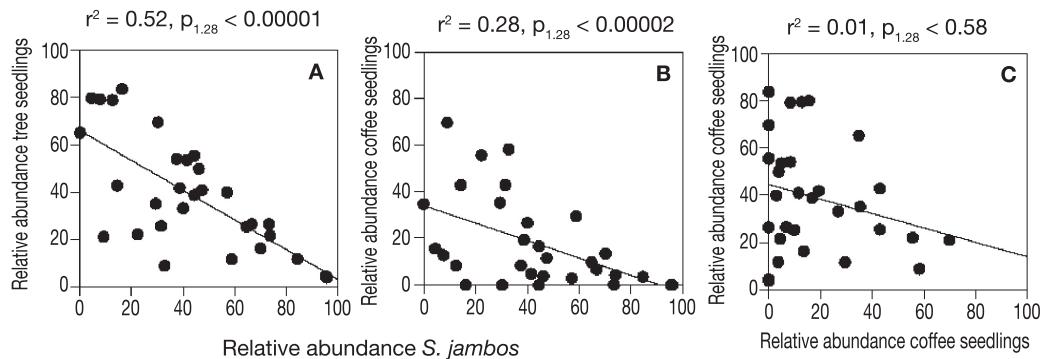


Fig. 1. Regression analyses of the abundance of *S. jambos* vs. the abundance of tree and coffee seedlings, and of coffee seedlings vs. the abundance of tree seedlings in the Municipal Forest of Atenas, Alajuela, Costa Rica.

we did not find a significant effect of variable levels of canopy aperture on the abundance of *S. jambos* seedlings ($r^2 = 0.002$, $p_{1,28} = 0.77$), abundance of tree ($r^2 = 0.0001$, $p_{1,28} = 0.94$) and coffee seedlings ($r^2 = 0.006$, $p_{1,28} = 0.67$). However, we observed the absence of *S. jambos* seedlings from sun-exposed forest edges and high light environments. It seems that seeds germinate and seedlings develop better under shade conditions (and thus, have difficulty colonizing open habitats), but to move to higher size classes, plants need a significant increase in radiation.

Population structure. The population distribution in size classes of *S. jambos* is dominated by seedlings under 50 cm in height (Fig. 2). Individuals above 1.5 m (juveniles and adults) were rare, although we detected 29 potential adults (individuals over 2 m, representing 4% of the sampled population) out of the total sample of 655 individuals. Although they were not represented in the sample, we observed more tall individuals on the edges of a coffee plantation. It is thus likely that the invasion into the Municipal Forest occurred through the reproduction of adults escaping from coffee plantations and farms, as well as by animal dispersal of fruits. This combined strategy is termed “infiltration invasion” by Wilson and Lee (1989). Fifty percent of the sampled population is less than or equal to 30 cm in

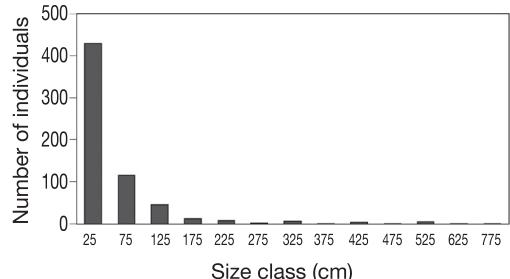


Fig. 2. Height distribution of individuals of *S. jambos* at the Municipal Forest of Atenas, Alajuela, Costa Rica.

height, 75% is under 64 cm, and only 10% is above 117 cm. The higher aggregation of seedlings took place around taller individuals.

DISCUSSION

Syzygium jambos had a clear negative impact on understory seedling diversity at the Municipal Forest of Atenas. Plots dominated by *S. jambos* had few seedlings from other species (including the other potential invader, coffee), which were concentrated in areas free from seedlings of *S. jambos*. Coffee seedlings are becoming abundant and are entering the forest as a result of dispersal by bats. Like *S. jambos*, coffee seedlings are also shade tolerant, and although they did not occur in such high numbers, over time they have potential to become

dominant in areas of the Municipal Forest that are close to coffee plantations (Fig. 1b). Shade tolerance gives *S. jambos* (and coffee) the capacity to invade even undisturbed forests, or forests in advanced stages of regeneration, as long as coffee plantations are nearby. Similar trends for shade tolerant invaders have been observed in temperate (Wyckoff and Webb 1996) and tropical areas (Meyer and Florence 1996). In addition, the low herbivory levels observed in *S. jambos* (DiStefano *et al.* 1998) due to the high tannin concentration could have the potential to deter the establishment of other tree seedling species due to allelopathic interactions, similar to the case of the introduced nitrogen-fixing tree *Myrica faya* that inhibits the germination of the native tree *Metrosideros polymorpha* on the island of Hawaii (Walker and Vitousek 1991). Since most of the understory is dominated by *S. jambos* (51% of all understory plants), it is very likely that the primary consequences of the invasion affect the first stages of regeneration of canopy trees, since areas dominated by *S. jambos* had a low density of canopy tree seedlings. Although the Atenas Municipal Forest is relatively large as compared to other forest fragments still surviving in the Central Valley of Costa Rica (i.e., DiStefano *et al.* 1998), it shares many of the problems of small fragments, such as the scarcity of reproductive adults, increased inbreeding depression, and recruitment limitation. To be of additional value to the local communities, these forests need to be managed to increase the level of diversity of understory seedlings, plant native trees by hand, and protect the forests from fire and from the invasion of exotic species. The removal of exotic species is recommended only if the local human communities want to preserve a sample of the original forest habitat by implementing restoration practices. If this is the case, the removal of exotics must be done cautiously with careful consideration of the maintenance of the ecosystem functions already being performed by exotics such as *S. jambos* (Westman 1990, Gordon 1998). These functions include production of food for vertebrates, soil stabilization, and

effects on water-holding capacity and water percolation of soils. It is very likely that a sudden removal of *S. jambos* will impact the water holding capacity of the soil, especially considering the steep topographic conditions present at the site. A much healthier strategy will be to begin selecting representative species of the area, establishing nurseries, and planting seedlings by hand, since forest isolation makes it unlikely that natural regeneration will proceed rapidly. At the same time, a consistent removal of seedlings and adults of *S. jambos* already in the forest should be implemented. More effective control programs at this stage will emerge from managing the entire forest from an ecosystem point of view, rather than focusing on individual species (Hobbs and Humphries 1994). We do not consider the introduction of biological control agents targeting *S. jambos* the best management strategy, due to the possibility that biological control agents may switch hosts over time and that one of the documented biological control agents, the fungus *Puccinia psidii*, is very aggressive (Tessman *et al.* 2001) and likely to switch hosts within the Myrtaceae (Rayachhetry *et al.* 2001). Although DiStefano *et al.* (1998) and Rayachhetry *et al.* (2001) did not find significant leaf damage provoked by this fungus, Tessman *et al.* (2001) report annual outbreaks of *Puccinia psidii* in Brasilia, Brazil, that cause major leaf, flower and fruit mortality. The elimination of large-scale mechanical removal and biological control as options leaves manual removal of *S. jambos* as the only suitable management technique for the Municipal Forest. A successful management plan would involve removal of seed sources outside the forest coupled with removal and replacement of *S. jambos* within. Adult *S. jambos* could be removed sparingly over time and replaced with native tree saplings. Removing saplings surrounding the adults is another possibility to ensure that species other than *S. jambos* will grow to adulthood. This will increase the overall diversity of native tree species by decreasing the sheer number of *S. jambos* saplings. A drawback to this plan is that it is highly time and labor-intensive, requiring

a devoted volunteer staff or long-term paid positions. It does, however, offer the ability to adjust management strategies in the short-term to address changes in the overall balance of the ecosystem.

ACKNOWLEDGMENTS

We thank Nolan Quirós for suggesting work on this system and the School for Field Studies for their logistic support during the period of the study.

RESUMEN

La fragmentación del hábitat, junto con otros disturbios antropogénicos, aumentan la vulnerabilidad de los ambientes nativos a la invasión por especies exóticas, agresivas y sin controles ecológicos. *Syzygium jambos* (L.) Alston (Myrtaceae, Manzana Rosa) es una invasora importante que todavía está extendiéndose en Hawaii, Las Antillas, Centro y Suramérica. Este estudio examina los efectos de *S. jambos* sobre la diversidad de plantas del sotobosque en un Bosque Húmedo Premontano de 25 ha en Atenas, Alajuela, Costa Rica, una microcuenca protegida que suple de agua potable a varias comunidades. Nuestro objetivo final es desarrollar una estrategia de manejo que combine la protección del agua con la conservación de una muestra representativa de la diversidad de plantas original del área. Distribuimos 30 parcelas de 2 X 2 m en el Bosque Municipal manteniendo una distancia mínima de 10 m entre parcelas y 2 m lejos de los senderos, para muestrear las plántulas y briznas de *S. jambos*, *Coffea arabica* (café) y árboles. Encontramos una clara dominancia de *S. jambos* sobre las demás plantas de sotobosque. De 1 285 plantas muestreadas *S. jambos* representó 51%, el café abarcó 14,78%, siendo el resto plántulas de árboles. *Syzygium jambos* tuvo la mayor densidad (5.46 plantas/m², D.E. = 6.44) en comparación a plántulas de árboles (3.67 plantas/ m², D.E. = 3.44) y de café (1.58 plantas/ m², S.D. = 2.13). Hubo una relación negativa entre la abundancia relativa de *S. jambos* y las plántulas de árboles ($r^2 = 0.52$, $p < 0.00001$) y café ($r^2 = 0.28$, $p < 0.002$). La abundancia de las plántulas de café no afectó la abundancia de las plántulas de árboles ($r^2 = 0.01$, $p < 0.58$). Ya que el dosel del Bosque Municipal es relativamente denso y se compone de una monocapa de árboles casi sin traslape entre copas, no encontramos relación entre la cobertura del dosel y la abundancia de *S. jambos*. La distribución de altura indicó que la mayoría de los individuos de *S. jambos* eran plántulas y briznas (altura ≤ 1.5 m), con solamente 4.6% clasificados como adultos, (altura ≥ 2 m). Los resultados

muestran un claro papel de *S. jambos* como especie invasora muy agresiva en el Bosque Municipal. Esta invasión es favorecida tanto por las características ecológicas de la especie así como por la fragmentación del bosque causada por plantaciones de café alrededor del sitio de estudio. Entre las diversas alternativas de manejo, consideramos que debe usarse una estrategia a nivel de ecosistema, y remover manualmente *S. jambos* a lo largo del tiempo y a la vez sembrar especies nativas, considerando que el uso programado para el Bosque Municipal es ser fuente de agua potable y proteger una muestra representativa de la vegetación original del área.

Palabras clave: *Syzygium jambos*, especies invasoras, manejo forestal, manejo de la calidad del agua, Costa Rica.

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