Germination and development of native species under the effect of allelopathic exudates of a superdominant species

Vera Lygia El Id[1], Nelson Augusto dos Santos Junior[2]

[1] Instituto de Pesquisas Ambientais, Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente. Doutora em Biodiversidade Vegetal e Meio Ambiente. https://orcid.org/0000-0001-5462-5004. E-mail: verinhalygia@gmail.com

[2] Instituto de Pesquisas Ambientais, Departamento de Apoio Técnico-científico. Doutor em Biologia Vegetal. https://orcid.org/0000-0002-9601-2350. E-mail: njunior@sp.gov.br

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Abstract

In plant dynamics, some species have an aggressive colonizing pattern (they may even become superdominant). This is the case of *Sesbania virgata* (Cav.) Pers., a shrub-tree species that, for a long time, was used in restoration programs due to its fast growth, short reproductive cycle, and little selectivity to unfavorable soil conditions. Thus, this study was carried out to analyze its allelopathic effect upon the seed bank of two native species with which it co-occurs in the environment. For this, seeds were collected from two *S. virgata* populations, one that produced and another unable to produce the allelochemical catechin (which is very abundant in this species). They were sown in 25-L pots with three substrate types under two development environments. After 16 months (during which the germination and development of the species were monitored), *Mimosa bimucronata* and *Peltophorum dubium* seeds were planted beneath *S. virgata* canopy and evaluated. *S. virgata* fully germinated in all environmental conditions but its height (above 100 cm versus 60 cm, on average) and diameter (above 18 mm versus 6 mm, on average) developed better under full sun than in the shade. *M. bimucronata* showed reduced n total germination values and speed when sown under *S. virgata* seedlings, with values from 40 to 50 % of those found without the presence of the latter species. *P. dubium* was tolerant of *S. virgata*. This pattern was also verified for early development. *S. virgata* may be used in restoration plantations, although it is necessary to consider its rapid development and allelopathic potential on some native species.

Keywords: *Sesbania virgata.* Allelochemical. Inhibitory species.

Introduction

The choice of correct species is an important tool in ecological restoration projects (Vidal, Rodrigues, 2019). However, generalist and aggressive native species can develop in a similar way to invasive ones, that is, these species start to excessively grow and multiply due to some environmental imbalance (usually caused by humans) (Pivello *et al.*, 2018).

These plants, called superdominant (Callaghan *et al.*, 2005; Matos and Pivello, 2009) develop intensively, negatively affecting other more sensitive native species. They can also alter natural ecosystem processes or even extinguish certain species (Lima *et al.*, 2012; Pivello *et al.*, 2018).

One of these species that has historically been highly recommended and used to restore areas degraded by mining is *Sesbania virgata* (Cav.) Pers. (Samôr *et al.*, 2002; Coutinho *et al.*, 2005; Florentino *et al.*, 2009; Sousa *et al.*, 2015). This heliophyte species has characteristics such as high germination and growth rates (Coutinho *et al.*, 2005; Souza *et al.*, 2010; Delarmelina *et al.*, 2013), fast reproductive cycle (Branzini *et al.*, 2012), and intense seed production, forming a seed bank with high longevity, efficient nutrient use (Nobrega *et al.*, 2008; Delarmelina *et al.*, 2014; Sousa *et al.*, 2015), defoliation tolerance, and high regrowth capacity (Carpanezzi, Fowler, 1997). Such characteristics make it a great competitor, providing it with successful establishment in mined areas with extreme abiotic conditions.

However, for the same reasons, the species can also be considered superdominant.

S. virgata belongs to the Fabaceae family. This pioneer is native to South America (Araújo *et al.*, 2004), being found in the South, Southeast, and Midwest regions of Brazil (in the Cerrado and Atlantic Forest biomes). It has also been documented in Paraguay, Argentina, and Uruguay (Pott, Pott, 1994). This species can produce allelochemicals, which have been found to inhibit germination and development of other plant species (Id *et al.*, 2015; Mignoni *et al.*, 2017; Araújo *et al.*, 2018).

Such inhibition can be attributed to some substances in *S. virgata*, such as the flavonoid (+)-catechin, which has a phytotoxic effect (Inderjit *et al*., 2008) and is present in various parts of the plant, such as its leaves (Id *et al.*, 2015) and seed integument, being released in large quantities in the first 24 hours after imbibition (Simões *et al.*, 2008).

The quantity of this metabolite can vary in *S. virgata* according to the plant organs and populations (Simões *et al.*, 2008; Id *et al.*, 2015; Id, Santos Junior, 2023b). Due to the conformation of the molecule, its effects depend on experimental conditions and target species sensitivity (Nijveldt *et al*., 2001). It may even alter the fungal community associated with the seeds (Id, Santos Junior, 2023a). Thus, understanding the role of these secondary metabolites in ecological processes such as allelopathy in plants requires that the dynamics and biological activity of secondary metabolites be studied in soil (Zhang *et al.*, 2011) — in which these substances also come into contact with other organisms (which can alter the reactions between species).

Attesting the effect of secondary metabolites in *S. virgata* plant material in uncontrolled experimental environments can help to better understand how this species adapts so well to the most diverse types of environment, even altering the composition of the community in which it is found since, in addition to its ecophysiological characteristics, some authors consider the production of allelochemicals as an advantage in competition with other species (Martins *et al.*, 2006; Barbosa *et al.*, 2008).

To assess these effects of this process, it is important to study them on species that co-occur with allelopathic species, in this case *Peltophorum dubium* (Spreng.) Taub. and *Mimosa bimucronata* (DC.) Kuntze (Id *et al.*, 2015), native tree species widely occurring in Brazilian forest formations (especially associated with environments with greater light availability and regenerating areas). *P. dubium*, known as *canafístula*, is a large tree that can reach more than 20 m in height. It has a wide and dense crown and mainly occurs in seasonal semideciduous forests and other formations in the Atlantic Forest, transition areas, and riparian forests. It is generally classified as a secondary or light-demanding species (Ferreira *et al.*, 2007), showing relatively rapid growth and potential use in restoration processes (Chagas Junior *et al.*, 2013; Portela *et al.*, 2001).

M. bimucronata, known as *maricá*, is a small to medium-sized tree often found in open areas, forest edges, *capoeiras*, and, above all, in humid environments, floodplains, and river banks. It has rapid growth, high capacity to occupy disturbed areas, and frequent association with early stages of ecological succession, being considered a pioneer species (Ferreira *et al.*, 2007). The ability to establish itself in altered environments and the occurrence in areas subject to flooding make *M. bimucronata* particularly relevant for recovering degraded environments and riparian forests.

Thus, this study was carried out to assess whether metabolites from *S. virgata* litters persist in the soil under natural conditions and to show its ability to affect the seed banks and

development of other plant species with which it co-occurs.

Material and methods

Obtaining the biological material - Fruits were collected from six *S. virgata* populations (Table 1), three of which with the presence of the (+)-catechin allelochemical in their plant material and three others in which the parts of their plants showed no such metabolite. All populations were in the municipality of Lavras (Minas Gerais State). Their characterization was based on preliminary studies (Id *et al*., 2015).

After collection, the fruits were processed and the seeds were separated into two lots according to their origin: the seed lots from catechin-producing (CP) populations and that from non-catechin producing populations (NP). The material was stored in a chamber at 25°C until the beginning of the analyses.

***S. virgata* germination and development** - *S. virgata* seed lots were manually scarified with the aid of sandpaper (P60 sheet) due to their dormancy (Camargos *et al*., 2008; Silva *et al*., 2011). They were then planted in 25-L pots using commercial substrate and deposited in two beds (one with 50 % shade and another under full sun) in the Seed Research Laboratory of the Institute for Environmental Research. Each shade treatment included 40 pots, 20 from the first batch (CP) and another 20 from the second batch (NP). A 2×2 factorial scheme (population × shade) was then constituted with four units in each replication and five replications for each treatment. The adopted design was entirely randomized.

In the first month after sowing, species germination was evaluated daily until it ceased, providing, at the end, germination percentage and speed index values (Maguire 1962), considering the emergence of the aerial part in the soil as germination. Stem height and diameter were measured to evaluate the development of *S. virgata* from the second month after sowing up to 16 months.

Quantification of catechin in soil samples - Soil samples were collected from the pots after 16 months of the experiment. The samples were randomly drawn and collected from two individuals from each of the five replications for each treatment to confirm the presence or absence of catechin. Samples of 1 g of soil were stored in sterile Eppendorf tubes, to which 1 mL of 100 % methanol was added. This material was briefly stirred in a vortex at maximum speed and sedimented by centrifugation for 10 minutes at 13,000 rpm. Then, the supernatant was collected and stored for analysis in high-performance liquid chromatography (Inderjit *et al*., 2008). For this, the collected materials were filtered in 0.45-μm Millipore filters and 20-μL aliquots applied in C18 column in a high-performance liquid chromatography Varian® system. Water and MeOH acidified with 0.1 % acetic acid (20 % to 100 % MeOH, flow rate of 0.8 mL min-1) was used in the separation. Detection was evaluated at 280-nm wavelength. (+)-catechin (Sigma) was used to construct the standard curve at varying concentrations for sample detection and quantification (Simões

Table 1. Geographical coordinates of the six catechin-producing and non-catechin producing populations.

	Catechin-producing populations	Non-catechin producing populations
Geographical coordinates	S21º 13' 35" W45º 00' 24" S21º 13' 27" W45º 00' 23" S21º 13' 16" W45º 00' 33"	S21º 12' 33" W45º 02' 07" S21º 15' 17" W45º 00' 46" S21º 15' 25" W45º 00' 40"

Source: authors (2026).

et al., 2008; Inderjit *et al*., 2008). The following equation was used for quantification: Y=6E+06X−8E+06; R^2= 0.96.

Early development of tree species co-occurrent with *S. virgata*

From a floristic survey of the tree species in the sample area, those with available seeds in the experimental period were searched; two selected species were obtained: *M. bimucronata* (DC.) Kuntze and *P. dubium* (Spreng.), the successional stage of which is classified as pioneer and secondary, respectively (Ferreira *et al*., 2007). The material was taken to the Seed Research Laboratory at the Institute of Environmental Research for processing and storage until assay configuration.

The seeds of both species were then planted in pots with well-developed *S. virgata* that deposited plant material on the soil to simulate a seed bank. The treatments and replicates were the same used for sowing *S. virgata*. Another 20 pots were also used to sow the seedlings of these species under full sun and shade without *S. virgata* seedlings, representing the control treatment of these species.

Data on germination percentage and speed index were collected (Maguire, 1962) during the first month after the two species were sown. To observe the effect of the contact of these species with the senescent leaf material of *S. virgata*, the initial development of these two plants was evaluated from the eighth month after *S. virgata* was sown up to the collection of height and diameter data. Data were collected every month for nine months.

All collected data were analyzed on SISVAR 5.1 (Ferreira, 2019) by analysis of variance. Means were compared by the Tukey's test ($p<0.05$). To express development over time, regression equations (expressed on lines) were adjusted by R^2 values.

Results and discussion

Germination and early development of *S. virgata*

The seeds of *S. virgata* germinated in full, regardless of origin (PC and NP) and shade, with no difference between germination conditions (Table 2). Likewise, the germination speed of the seeds of the species was high (with no difference between the tested conditions). Silva *et al.* (2011) and Id, Santos Junior (2023b) — studies with *S. virgata* seeds — found that seed germination nears 100 % and a high germination speed index as long as dormancy is broken.

Table 2. Mean germination percentage and speed index values of *S. virgata* seeds from catechin-producing (CP LOT) and non-catechin producing populations (NP LOT) under full sun and shade.

	Environments			
Origin	**Full Sun**	**Shaded**	**Full Sun**	**Shaded**
	Germination Percentage		**Germination Speed Index**	
CP Batch	100 a	100 a	0.08125 a	0.08030 a
Lote NP	100 a	100 a	0.09095 a	0.08595 a

Obs: Averages followed by the same letter fail to differ from each other by the Tukey's test at the 5 % probability level. Lowercase letters analyze the environment factor within a provenance date.

Source: authors (2026).

Figure 1. Average biometric data for the height (cm) and diameter (mm) of *S. virgata* seedlings from CP (A and C) and NP seeds (B and D) under full sun (red line) and shade (blue line).



Source: authors (2026).

Regarding species development (Figure 1), *S. virgata* seedlings had gradual gains in height (Figures 1A and 1B) and diameter (Figures 1C and 1D) under full sun over the 16 months of evaluation regardless of origin (Figures 1A and 1B, respectively). Observing the development of *S. virgata* seedlings of both shaded lots shows that the height growth (Figures 1A and 1B) was initially similar under full sun, remaining stable up to the tenth month, from which the average height of the CP and NP lot seedlings gradually decreased until the end of the experiment evaluation. This development habit was also verified in the data on seedling diameter (Figures 1C and 1D) since the average diameter decreased after stagnation (around the 11th month).

Chaves *et al.* (2003) mention the potential of this pioneer species for programs to recover degraded areas due to its ease of propagation (high germination and growth rates), a fact also verified by Id and Santos Junior (2023b), who found that the species developed well in any soil condition (but more so in full sun).

Germination and early development of the co-occurring species

P. dubium seeds steadily germinated regardless of condition, with percentages ranging from 75 to 100 %. Id *et al.* (2020) also found that *P. dubium* germination underwent no significant changes in relation to *S. virgata* plant material substances. Germination speed index values occurred in a similar way, with a significant increase in the germination speed index from 0.109 to 0.163 in seeds germinated under full sun. *P. dubium* germinated under shade only in the NP lot (Table 2). *P. dubium*, classified as a secondary species, better tolerates shade (Portela *et al.*, 2001), which may justify its

better germination speed under such conditions in this study.

Regarding *M. bimucronata* germination (Table 2), the germination percentage and emergence speed index of seeds under full sun were negatively affected in pots with *S. virgata* seedlings when compared to the control group. Values of 55 and 65 % were recorded in the seeds germinated in the CP and NP lot pots, whereas the germination of the control pot was 95 %. Essays by Id *et al.* (2020) also found the negative interference in the germination of *M. bimucronata* seeds in contact with aqueous *S. virgata* extracts and the application of extracts produced with commercial catechin.

The sowing environment also had a significant interference in the percentage of germination of *M. bimucronata* seeds in CP lot seedling pots, in which values of 55 % in full sun and 95 % in shade were recorded. The same happened for the *M. bimucronata* seeds in NP lot pots; values equal to 65 % under full sun and 95 % under the shade. Within the same environmental condition, lot origin interfered in germination speed indices, that is, different significant values were recorded for the germinated seeds in CP and NP lot pots. When analyzing the influence of the full sun and shade conditions, statistical differences were also observed within the CP and NP lots and the control treatment (Table 3).

Figure 2 illustrates the development of *P. dubium*, showing differences in the growth of its plants according to the environmental condition. Regarding the height of *P. dubium* under full sun (Figure 2A), the seedlings in pots containing CP lot *S. virgata* plants had higher values in the same period than the *P. dubium* seedlings in the control pots and in those with NP lot plants. It was also noted that the *P. dubium* seedling diameter followed the height growth pattern: the highest found diameter values were those of *P. dubium* seedlings in CP lot pots, followed by the control pots and those with *S. virgata* seedlings from the NP lot (Figure 2C).

Under shade (Figure 2B), the result was the opposite as the *P. dubium* seedlings with the

Table 3. Average values referring to germination percentage and speed index of *P. dubium* and *M. bimucronata* in pots containing *S. virgata* plants from catechin-producing (CP Lot) and non-catechin producing populations (NP Lot) and pots without *S. virgata* (control) under full sun and shade.

	P. dubium		***M. bimucronata***	
	Environments			
Origin	**Full Sun**	**Shade**	**Full Sun**	**Shade**
	Germination percentage			
CP Lot	80 Aa	75 aA	55 aA	95 bA
NP Lot	80 Aa	100 aA	65 aA	95 bA
Control	85 aA	80 Aa	95 aB	95 aB
	Germination Speed Index			
CP Lot	0.128 aA	0.098 aA	0.093 aA	0.174 bA
NP Lot	0.109 aA	0.63 Bb	0.125 aA	0.186 bA
Control	0.103aA	0.101aA	0.187aB	0.241aB

Obs: Averages followed by the same letter fail to differ from each other by the Tukey's test at 5 % probability. For each species, lowercase letters compare the environments within each origin and uppercase letters compare origins within each environment.

Source: authors (2026).

Figure 2. Average height (cm) and diameter (mm) biometric data values of *P. dubium* germinated under full sun (A and C) and shade (B and D) in pots containing *S. virgata* seedlings from CP (red line) and NP lots (blue line) and in pots without *S. virgata* seedlings (green line) from May 2019 to January 2020.



Source: authors (2026).

higher average height values in the same period were those that were in pots containing CP lot *S. virgata* plants, followed by those in the control pots and in CP lot pots. Analyzed under shade (Figure 2D), it was observed that the average diameter values of *P. dubium* seedlings, within nine months, were more accentuated for the seedlings in pots with *S. virgata* plants belonging to the NP lot, followed by the seedlings in control treatment and in CP lot pots, as observed in the height growth of these seedlings.

The low effect of these substances on *P. dubium* seeds may be related to the fact that species that co-occur in the environment with other species with superdominant potential acquire resistance to them during the evolutionary process (Id *et al.*, 2020). Another possible explanation for the adequate development of *P. dubium* seedlings in pots containing CP lot *S. virgata* seedlings, in addition to the environmental conditions appropriate to the species to which they were exposed, is in the work of Id *et al.* (2020), who showed that applying aqueous *S. virgata* leaf extracts increased biometric variables in native tree species. This increase probably stems from the fact that the used plant material, rather than only consisting of harmful molecules such as catechin, include other secondary metabolites, some of which can aid seedling nutrition (Maraschin-Silva, Aquila, 2006).

Analyzing the development of *M. bimucronata* seedlings (Figure 3) shows that, regarding the control treatment seedlings, the average *M. bimucronata* height values showed high and gradual growth, more so in seedlings in pots of the NP lot and under full sun (Figure 3A) in relation to the values for the same treatments and period under shade (Figure 3B), precisely

because the species is considered a pioneer (Ferreira *et al.*, 2007).

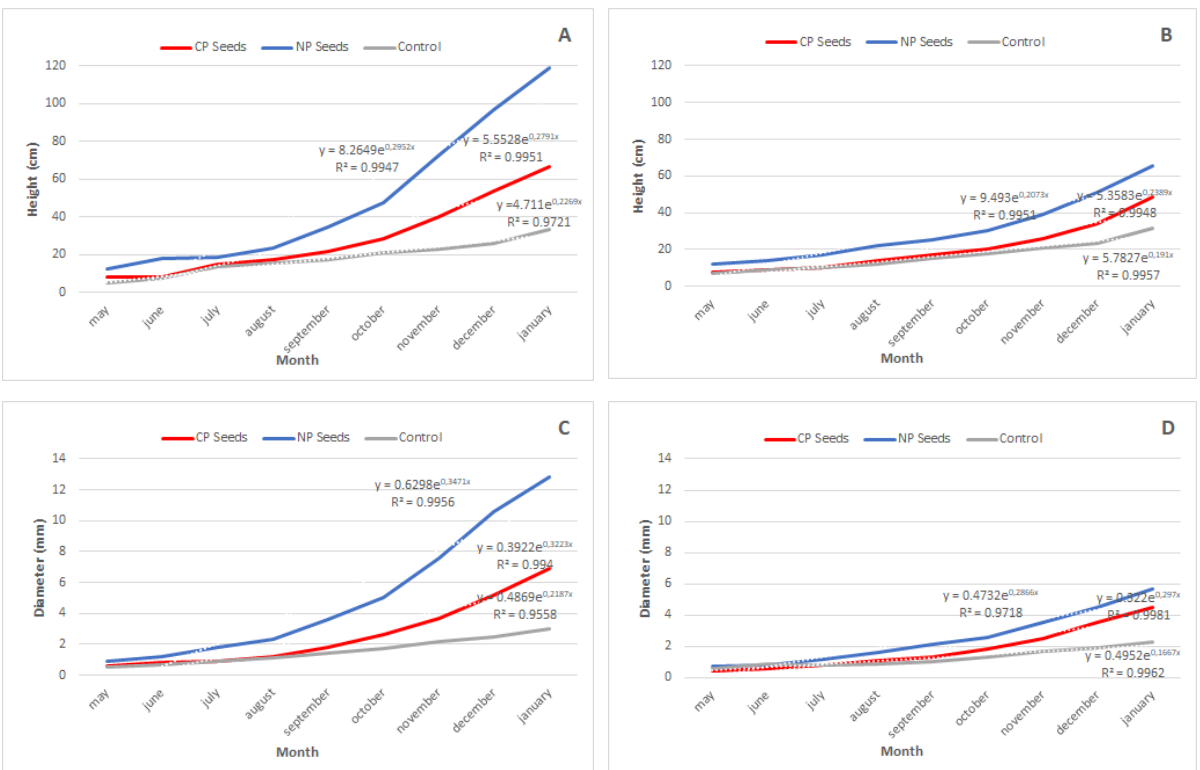
The same was observed for the mean *M. bimucronata* diameter values when compared between treatments and environmental conditions (Figure 3). Under full sun, a gradual increase in diameter was observed in the evaluated period, being higher for NP lot seedlings (Figure 3C). This growth behavior was also observed under shade (Figure 3D) but less than in seedlings under full sun. Observing the axes of the graphs in Figure 3, the average values of height and diameter of *M. bimucronata* were higher under full sun for the three treatments. Its better development in NP lot pots than in CP lot ones can be explained by the factors regarding the greater development of CP lot seedlings in full sun, in which it is expected that these seedlings have produced greater amounts of leaf material containing allelochemicals such as catechin, thus altering the development of *M. bimucronata.*

Conclusions

It is concluded that the allelochemicals associated with *S. virgata* last in the soil and exert a direct but distinct influence on the seed banks and development of co-occurring species. While *S. virgata* maintains high germination capacity and full development in full sun, prolonged shade severely limits the growth of its seedlings.

The secondary species *P. dubium* was tolerant to *S. virgata* metabolites, maintaining high germination rates and good vegetative development. This pattern suggests a possible evolutionary adaptation to living with the species or a beneficial effect promoted by the nutrition from the organic matter of the litter.

Figure 3. Average height (cm) and diameter (mm) biometric data for *M. bimucronata* germinated under full sun (A and C) and shade (B and D) in pots containing *S. virgata* seedlings from CP (red line) and NP lots (blue line) and in pots without *S. virgata* seedlings (green line) from May 2019 to January 2020.



Source: authors (2026).

On the other hand, *M. bimucronata* had its germination and emergence speed significantly inhibited by the presence of more vigorous *S. virgata* seedlings in full sun, a condition in which the production of inhibitory metabolites is intensified.

Thus, the allelopathic effects of the *S. virgata* leaf litter vary according to the degree of sensitivity of the neighboring species and environment conditions.

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