Article

Analysis of Reproduction and Natural Regeneration of *Psidium cattleianum* Afzel., an Invasive Species in Eastern Madagascar

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Abstract

Psidium cattleianum Afzel. ex-Sabine (Myrtaceae) is an invasive alien species occurring in the Betampona Nature Reserve in eastern Madagascar, where it disrupts native vegetation. This study aimed to analyse its phenology and evaluate its natural regeneration capacity. A phenological assessment was carried out, combined with the setting up of sampling plots for floristic inventories in *savoka* ecosystems dominated by *P. cattleianum*. Field observations enabled the identification of dispersal agents, while three plots were used to quantify natural regeneration. Phenological results indicate a vegetative phase from May to October, flowering from November to March, and fruiting from November to May. The main dispersal vectors include runoff water, *Eulemur fulvus albifrons*, *Potamochoerus larvatus*, *Alectroenas madagascariensis*, and human activities. The density of *P. cattleianum* ranges from 4 to 11 individuals per square metre, with strong natural regeneration. Compared to *Harungana madagascariensis* and *Treculia africana*, the species

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develops a more vigorous root system from the seedling stage onward. Following ANOVA testing, cutting and artificial wounding produced a significantly higher number of sprouts than girdling. No significant difference was observed between girdling and natural wounds. Significant differences were found among classes 1, 2, 3 and 4 (p). The applied treatments showed an increase in bud production with increasing stem diameter. A wound of 4 cm² healed within approximately eight months. These results have important implications for the practical management of the reserve. Accordingly, control of this species can be achieved through manual uprooting, cutting, girdling (ringbarking), and active ecological restoration.

Keywords: phenology; natural regeneration; invasive species; *Psidium cattleianum*; Betampona Nature Reserve

1 Introduction

Biological invasions are recognised as one of the major environmental challenges at the global scale. They affect a wide range of ecosystems, from boreal and temperate zones to tropical regions. The consequences of these phenomena extend far beyond ecological impacts, also generating significant economic and social effects. Indeed, certain invasive species can cause economic losses, such as reduced agricultural yields (for example, *Centaurea solstitialis* in California). Invasions also contribute to the degradation of ecosystem services through mechanisms such as landscape transformation, soil erosion, and reduced water availability [1], [2].

From an ecological perspective, these species often limit the growth and development of native species, which are generally less competitive [3], and may force some species to migrate to other habitats [4]. This contributes to a decline in species richness and, more broadly, to the erosion of local biodiversity [5]. Madagascar, recognised as one of the world's biodiversity hotspots, is distinguished by exceptionally high levels of diversity and endemism across major taxonomic groups [6]. The Betampona Nature Reserve is a protected area characterised by remarkable floristic richness, estimated at 68 plant species per 100 m² [7]. However, despite its richness, the reserve is currently facing the proliferation of invasive alien plant species, which pose a significant threat to biodiversity conservation [8]. Among these species is *Psidium cattleianum* Afzel. ex-Sabine (Myrtaceae), whose expansion is of increasing concern to reserve managers [9]. They estimate that, without targeted intervention, the floristic composition of the reserve could be profoundly altered within the next two decades. The study of the phenology and natural regeneration capacity of *Psidium cattleianum* in the Betampona Nature Reserve is therefore part of an effort to better understand the mechanisms underlying its expansion. Previous studies conducted in the Ranomafana National Park have already addressed issues related to this species [10], while Birkinshaw [11] highlighted the role of its fruits in the diet of several animal species, potentially contributing to its dispersal.

The present study, resulting from a collaboration between the Plant Biology and Ecology programme of the Faculty of Sciences at the University of Antananarivo, the Madagascar Fauna and Flora Group, and the technical manager of the Betampona Nature Reserve, aims to analyse the reproductive and regenerative characteristics of *Psidium cattleianum* through a phenological and ecological approach. The main objectives of this research are to describe the phenological cycle of the species, identify its natural regeneration capacity, and determine the ecological factors that favour its establishment and spread. To this end, two hypotheses were formulated:

H1: *P. cattleianum* exhibits a biannual phenological cycle in disturbed environments.

H2: The species shows a high regeneration rate regardless of the topographic gradient.

The structure adopted to test these hypotheses follows the IMRAED format, which will be presented sequentially below.

2 Study Area

The Betampona Nature Reserve is located approximately 40 km northwest of the city of Toamasina in Madagascar, spanning the municipalities of Sahambala and Ambodiriana. It extends between 17°51′ and 17°55′ South latitude and 49°10′ and 49°15′ East longitude. The reserve covers an area of 2 228 ha. Currently, about 470 ha consist of secondary forests, two-thirds of which are dominated by invasive or undesirable species forming the majority of the *savoka* (secondary vegetation), including *savoka* dominated by *Psidium cattleianum*, *Solanum mauritiana*, and *Aframomum angustifolium*.

3 Materials and Methods

An invasive plant is defined as any exotic species introduced, either directly or indirectly, by human activities and occurring outside its native range. It becomes a dominant, naturalised and transformative species, inducing functional and structural changes in ecosystems or natural habitats [9]. The plant material used in this study is the invasive species *Psidium cattleianum*, whose taxonomic classification is as follows:

Kingdom: Plantae

Division: Magnoliophyta

Class: Magnoliopsida

Order: Myrtales

Family: Myrtaceae

Genus: *Psidium*

Species: *cattleianum* Afzel. ex-Sabine

Vernacular names: Chinese guava; *Goavitsinahy* (local name)

3.1 Phenological Study

The main phenological stages include emergence, leaf development, tillering, stem elongation, inflorescence formation, flowering, fruit development, maturation, and senescence [12]. In this study, the phenological status of *Psidium cattleianum* was monitored in relation to the mean annual temperature from August 2010 to July 2012. Ten individuals were observed monthly in each of three 30 m × 30 m plots (flowering, fruiting, and vegetative stages), and the results were recorded. In addition, the number of fruits produced per individual was also recorded during the fruiting season.

3.2 Natural Regeneration Capacity

Natural regeneration refers to all processes by which plants reproduce naturally without silvicultural intervention [13]. The study of natural regeneration makes it possible to determine species density relative to a given area, and its regeneration rate.

Regenerated individuals and seed-producing individuals of this species present in three plots, each with an area of 250 m², and were counted separately across three different topographic positions: upper slope (Site 1), mid-slope (Site 2), and lower slope (Site 3). In this study, seed-producing individuals are defined as those with a height greater than or equal to 3 m, whereas individuals with a height less than 3 m are considered regenerated individuals.

The regeneration rate (RR) is defined as the percentage of regenerated individuals (*Nr*) relative to the number of seed-producing individuals (*Nsp*) [14]. It is expressed by the following formula:

$$RR(\%) = \frac{Nr}{Nsp} \times 100$$

Accordingly, if the RR is less than 100%, the species is considered to have poor regeneration. If RR ranges between 100% and 1 000%, the species exhibits moderate regeneration, and if RR exceeds 1 000%, the species is considered to have good regeneration.

The mode of seed dispersal and the spread of seeds in the natural environment were also analysed. For this purpose, 30 individuals were monitored for fruit production, and the number of fruits produced per individual was recorded.

3.3 Species' Adaptation Capacity

Adaptation can be generally defined as the functional adjustment of an organism to its environment, and more specifically as the suitability of organs to their functions. It allows the organism to maintain coherence with the environment in which it develops. The invasiveness of the studied species varies considerably depending on the habitat [15]. Three aspects of adaptation were evaluated:

a) Adaptation through sprouting and stem development following two distinct treatments: stem cutting and bark removal. The results were analysed according to four stem diameter classes. The diameter classes considered are as follows: Class 1:]1.5 cm: 2.5 cm [; Class 2:]2.5 cm: 5 cm [; Class 3:]5 cm: 8 cm [; Class 4:]8 cm: + [

b) Comparison of different root types, distinguishing Type I, II, and III roots, in relation to the root systems of two native species: *Treculia africana* (Moraceae) and *Harungana madagascariensis* (Clusiaceae). This comparison was conducted to assess the potential correlation between the root development of *Psidium cattleianum* and its capacity to establish in infested areas.

c) Artificial wounding of the *Psidium cattleianum* trunk using a square incision of 2 cm per side, to evaluate the time required for complete wound closure and to monitor the condition of the species during the observation period. The experiment was conducted on 10 plants with stem diameters ranging from 4 to 6 cm. Figure 1 shows the monitoring of the growth of the coating. The data were collected monthly.

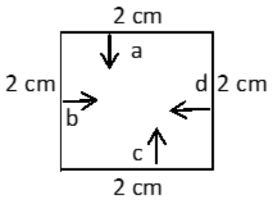

Figure 1: Monitoring of the growth of the coating

4 Results

4.1 Phenology of *Psidium cattleianum*

Figure 2 shows the phenological diagram of *Psidium cattleianum* in relation to temperature variations in the region.

The species exhibits a vegetative stage from June to October, although its leaves remain green throughout the year. Flowering occurs from November to March, with peak intensity in December and January. Fruiting also begins in November, reaching its maximum in February and March. Fruits mature between March and May, marking the end of the fruiting period. Outside the reserve, personal observations indicate that some individuals may undergo a second fruiting period in September and October.

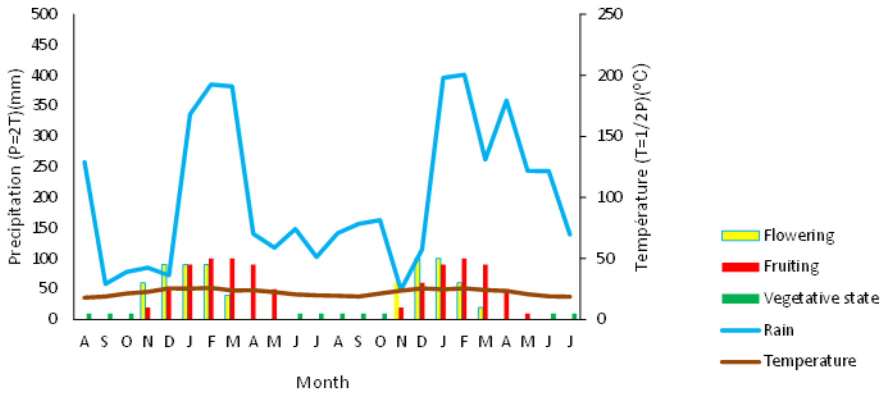

Figure 2: Phenological diagram according to temperature and precipitation (2010–2011–2012)

Regarding temperature conditions, flowering and fruiting of *Psidium cattleianum* are favoured by temperatures ranging from 21.4 °C to 25.6 °C, corresponding to the period from November to May. Under these conditions, all phenological stages are present, and in very open habitats, some individuals exhibit bimodal fruit production, supporting hypothesis H1.

4.2 Natural Regeneration of the Species

On average, a seed-producing individual can produce 69 fruits. The number of seeds per fruit ranges from 4 to 36. The main natural dispersers in the reserve include runoff water on slopes, the lemur *Eulemur fulvus albifrons*, the wild pig *Potamochoerus larvatus*, the bird *Alectroenas madagascariensis*, and human activities.

The density per square metre and the RR are presented in Table 1.

Table 1: Density and regeneration rate of the species

Site	Site 1	Site 2	Site 3	Moyenne
Area	250 m^2	250 m^2	250 m^2	250 m^2
Number of individuals	1 186	1 172	2 981	1 779,67 ± 1 040,40
Species density	4 744	4 688	11 924	7,11 ± 4
Seed-producing individuals	58	181	375	204,67 ± 159,506
Regenerated individuals	1 128	991	2 606	4 725 ± 969,095
RR (%)	1 944,81	547,51	694,93	1 062,41 ± 767,7

According to Table 1, the species density ranges from 4 to 11 individuals per square metre. At Site 1, *Psidium cattleianum* shows good regeneration, whereas at Sites 2 and 3, the species exhibits moderate regeneration. Seed dispersal of *Psidium cattleianum* occurs primarily through its seeds. At the end of the fruiting period, approximately 70–80% of the fruits fall to the ground within a radius of about 10 metres around the parent plants. Seed dispersal can be classified as either zoochorous (mediated by animals) or barochorous (mediated by gravity), depending on the mode of diaspore deposition.

4.3 Adaptability of the Species

4.3.1 Bud Development

The results of bud development, analysed using the Kruskal–Wallis test, are presented in Figure 3.

Treatments involving cutting generated a significantly higher number of shoots compared to bark removal ($\rho = 2 \times 10^{-16} < 0.05$) and natural wounds ($\rho = 2 \times 10^{-16} < 0.05$). These results indicate a significant difference in bud development between the cutting treatment and the other two treatments (bark removal and natural wounds). In contrast, no significant difference was observed between bark removal and natural wound treatments ($\rho = 0.14 > 0.05$). Regarding stem diameter classes, significant differences were observed between the classes]1.5–2.5],]2.5–5],]5–8], and]8–10] ($\rho = 2 \times 10^{-16} < 0.0001$), particularly between the]1.5–2.5] class and each of the other classes. These results suggest that *Psidium cattleianum* possesses a rapid regeneration capacity, regardless of the type of trauma experienced. This accelerated growth dynamic is especially evident following major disturbance events such as cyclones, earthquakes, or clearing activities.

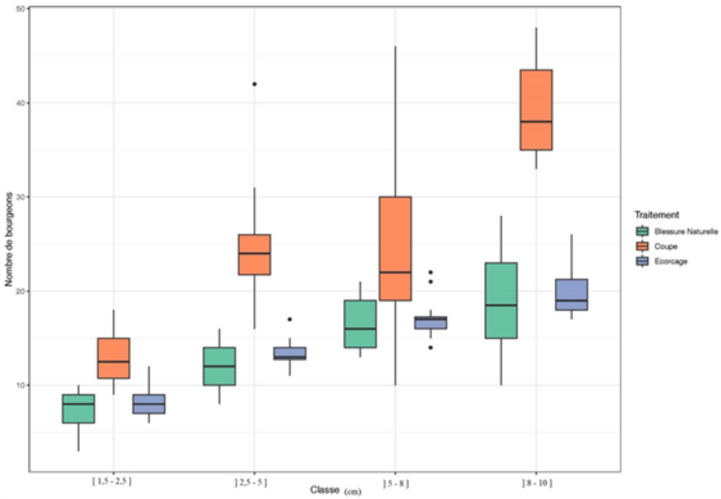

Figure 3: Box plot of bud development under different treatments

4.3.2 Seedling Root Development

Table 2 presents the results comparing the number of roots of *Psidium cattleianum* with those of selected native species.

Table 2: Comparison of root development of *Psidium cattleianum* with native species

Species	Number of individuals	Mean height (cm)	Mean number of roots		
			I	II	III
Treculia africana	10	17	1	10,5	10,3
Harungana Madagascariensis	10	9,71	1	21,1	21,1
Psidium cattleanum	36	24	1,02	38,78	28,92

Psidium cattleianum exhibits particularly extensive root development, especially in Type I, II, and III roots. This species also stands out for its stem growth rate, which is markedly higher than that observed in *Treculia africana* and *Harungana madagascariensis*. This enhanced root production capacity may provide an adaptive advantage, allowing *Psidium cattleianum* to grow rapidly in nutrient-poor soils and to establish successfully in open and degraded forest habitats. Furthermore, the presence of this species appears to exert strong competitive pressure on neighbouring plant species, compromising their survival and growth. The healing rate of the wounded area is presented in Figure 4.

Complete healing of a wound with a surface area of 4 cm² occurs within eight months, and the wounds do not cause disease or plant mortality.

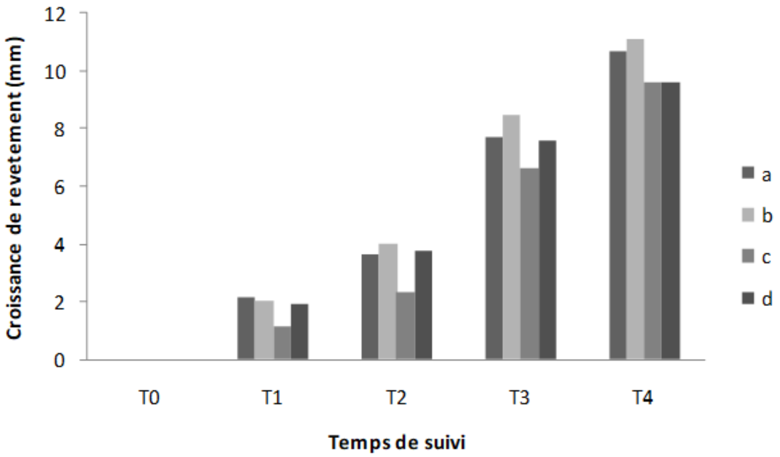

Figure 4: Histogram of healing rate on each side

5 Discussions

In this study, it appears essential to control the spread of *Psidium cattleianum* in the Betampona Nature Reserve, based on the available phenological and ecophysiological data for this species.

5.1 Reproductive Strategy and Ecological Plasticity

The results obtained indicate that *Psidium cattleianum* exhibits a particularly effective reproductive strategy in the Betampona Nature Reserve. The average production of 69 fruits per individual, combined with 4 to 36 seeds per fruit, demonstrates a strong potential for sexual multiplication. The prolonged fruiting period (November to May), along with the observation of a second fruiting in disturbed habitats, suggests significant phenological plasticity. This temporal flexibility constitutes a major adaptive advantage in tropical environments subject to interannual climatic variations. Successful invasive species typically combine high fecundity, effective dispersal, and broad ecological amplitude [16], characteristics clearly observed in *P. cattleianum*, contrary to the assertion by Iambana [17] that October heat and decreased humidity favour leaf drop. Zoochory, involving *Eulemur fulvus albifrons*, *Potamochoerus larvatus*, and *Alectroenas madagascariensis*, amplifies seed dispersal beyond the parent plant, facilitating rapid colonisation of forest gaps. Furthermore, the vegetative regeneration capacity observed after cutting or wounding indicates a dual reproductive strategy (sexual and vegetative). This combination enhances the species' resilience to natural disturbances (cyclones) and anthropogenic disturbances (clearing activities). Therefore, *P. cattleianum* does not rely exclusively on seed production for persistence, which significantly complicates control efforts. In Madagascar, despite exceptional endemic species richness, biological invasions remain poorly studied [18] and are rarely integrated into national environmental policies [19].

5.2 Root Competitive Advantage and Ecological Dominance

Comparative analysis of root development shows that *P. cattleianum* develops a denser and more vigorous root system than *Treculia africana* and *Harungana madagascariensis*. This early development, starting from the seedling stage, provides the species with a competitive advantage in acquiring water and nutrients. In *savoka* and degraded secondary forests, where competition for nutrients is intense, this structural advantage facilitates its rapid establishment. The high observed density (up to 11 individuals/m²) reflects this capacity for aggressive spatial occupation. High biomass is consistently observed throughout the year for *P. cattleianum*. Phenology provides essential information for predicting biomass, fruit number, and seed weight [20], making it useful for agricultural applications [21]. Moreover, the rapid wound-healing capacity (eight months for a 4 cm² wound) indicates high tolerance to mechanical stress. This resistance to trauma allows the species to survive disturbances and quickly resume growth. According to the theory of dominant invasive species [22], the combination of an efficient root system and rapid growth promotes monopolisation of available ecological niches. Consequently, the presence of *P. cattleianum* may progressively reduce recruitment of native species [23], threatening the natural dynamics of the forest.

5.3 Operational Implications for Management

The results obtained provide concrete guidance for shaping management strategies in the Betampona Nature Reserve. The species' strong resprouting capacity after cutting suggests that simple felling, without follow-up, is likely to be ineffective. Bark removal (girdling) appears to be a potentially more appropriate method when applied correctly and monitored over time. Manual removal of young plants constitutes a relevant option in recently colonised areas. However, given the extremely high RR (> 1 000% at certain sites), any intervention must be repeated and integrated into a long-term management plan. Active restoration through planting competitive native species could limit recolonisation by rapidly occupying space and reducing light availability. Differentiated management according to the topographic gradient (upper versus lower slope) could also optimise allocation of effort. Finally, involvement of local communities is essential to limit anthropogenic dispersal and ensure continuous monitoring. Management of *P. cattleianum* therefore cannot rely solely on mechanical control; it must combine control measures, ecological restoration, and adaptive monitoring.

In summary, the invasive success of *Psidium cattleianum* relies on a combination of high reproductive plasticity, early root competitive advantages, and strong tolerance to disturbances. These characteristics explain its increasing dominance in the secondary forests of eastern Madagascar. Therefore, an effective management strategy must be integrated, progressive, and based on the ecological mechanisms highlighted by this study.

6 Conclusion

The phenological study conducted between 2010 and 2012 on *Psidium cattleianum* provided a deeper understanding of the biological and ecological characteristics of this species. The observed phenological cycle shows that the vegetative phase extends from June to October, while flowering and fruiting begin in November. Fruit maturity is reached between March and May. Flowering and fruiting are favoured by temperatures ranging from 21.4 °C to 25.6 °C. All phenological stages were observed, and some individuals of *P. cattleianum* at forest edges often undergo two reproductive cycles per year, confirming the first hypothesis of this study.

Seed dispersal occurs primarily through zoochory, barochory, and human-mediated mechanisms. In addition, stem contact with the soil, particularly following disturbances by animals, and cyclones or other events, contributes to the formation of dense and competitive root networks. *P. cattleianum* possesses remarkable natural vegetative multiplication capacity. This morphological plasticity, combined with high adaptability in disturbed environments from upper to lower slopes, largely explains the high density of the species in the Betampona Nature Reserve. These results confirm the second hypothesis of this study, showing that the species can multiply across all open topographic environments. However, this colonisation dynamic poses a potential threat to native species, highlighting the need for integrated approaches that combine mechanical control and ecological restoration. Eradication of *P. cattleianum* remains a complex task, requiring targeted, progressive, and carefully monitored actions: manual removal in small areas, trunk cutting, girdling, followed by the restoration of native species. These operations require careful planning with regard to labour, time and budget. Regular monitoring is essential to remove resprouts and seedlings.

In conclusion, although certain management techniques have shown potential, the issue of controlling *P. cattleianum* remains unresolved and warrants increased attention in future research.

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