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# ECOLOGICAL AND BIOLOGICAL BARRIERS TO THE EX SITU PROPAGATION OF VACCINIUM FLORIBUNDUM KUNTH: ASSESSING SEXUAL AND ASEXUAL LIMITATIONS FOR DOMESTICATION

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## ABSTRACT

***Vaccinium floribundum Kunth (mortiño) is a key species for Andean ecosystem conservation with high commercial potential. However, its domestication is hindered by complex propagation requirements. This study evaluates the limitations of sexual and asexual reproduction under nursery conditions in Chimborazo, Ecuador. A factorial 23 design was implemented to test seeds (subjected to cold storage) and rhizomes (treated with IBA at 400 mg L ¬¹ and different substrates). Results revealed a total absence of germination (0%) in seeds, likely due to deep physiological dormancy and the loss of viability during storage. In rhizome propagation, a maximum survival rate of 25% was observed only in paramo soil substrates without IBA, while higher concentrations of exogenous hormones and peat-based substrates negatively affected rhizogenesis. These findings suggest that V. floribundum exhibits recalcitrant behavior and high substrate specificity, indicating that current ex situ protocols are insufficient. Domestication efforts must shift toward mycorrhizal inoculation and advanced dormancy-breaking techniques to overcome these biological bottlenecks.***

**KEYWORDS:** Dormancy-breaking; Rhizogenesis; Ex situ bottlenecks; High-altitude Ericaceae; Indole-butyric acid (IBA); Paramo conservation.

## 1. INTRODUCTION

Globally, interest in the Vaccinium genus has grown exponentially, driven by the recognition of its berries as superfoods with exceptional therapeutic properties (Vega-Polo et al., 2020; Welch et al., 2008). Specifically, the Andean blueberry or mortiño (Vaccinium floribundum Kunth) is highly valued for its exceptional antioxidant capacity, attributed to its rich profile of phenolic compounds and anthocyanins, which frequently surpass those of commercial blueberries (Schreckinger et al., 2010; Vasco et al., 2008). Ecologically, V. floribundum is a keystone species in the high-altitude Andean paramo (3000–4500 masl.), playing a critical role in soil retention, watershed protection, and providing vital food resources for endemic frugivorous fauna (Luteyn, 2002). Despite its socioeconomic and ecological importance, wild populations are increasingly threatened by climate change, habitat fragmentation, and uncontrolled extractive harvesting (Cuesta et al., 2017; Ticktin, 2004). Consequently, domesticating wild Vaccinium species has become a global conservation priority; however, this transition from wild to cultivated environments is frequently hindered by profound physiological propagation bottlenecks (Cobo et al., 2018).

In Ecuador, the mortiño (V. floribundum Kunth) is also identified as a species with significant economic potential, given its nutritional composition (Meléndez-Jácome et al., 2021), antioxidant properties (Guevara-Terán et al., 2022; Rojas-Ocampo et al., 2021), potential medicinal applications (Baenas et al., 2020; Ruilova et al., 2022), and cultivation techniques (Llivisaca-Contreras et al., 2022). Despite its nutritious fruits that are unique to Andean mountains, the potential of this species remains undeveloped. Commercial plantings for the native blueberry are not well document, and it is typically found in clonal colonies in the wild (paramo mountain chaparros) Wild Vacciunium species exhibit low genetic variability compared to their counterparts, which display higher variability. As such, domestication of the wild species is necessary to enable year-round production in various locations (Gutiérrez Madrid & Camacho Campos, 2011).

High Andean ecosystems inhabitants, recognizing potential of the mortiño, have begun an unsustainable extraction process transplanting plants from their natural habitats to ex-situ conditions. This practice disrupts ecological balance and affects other dependent plants (Llivisaca-Contreras et al., 2022). Such exploitation is common for several Ericaceae family species due to the lack of adequate propagation methods. Despite the plant significance, research efforts and information on its propagation are scarce (Gutiérrez Madrid & Camacho Campos, 2011).

Asexual propagation methods include cuttings, layering, tissue culture and division. Plants within this genus have a strong regenerative capacity, allowing to produce uniform progeny through cloning. This approach aims to preserve the genotype, though factors such as diseases and mutations can negatively impact reproduction.

However, the transition from wild harvesting to controlled cultivation of V. floribundum faces significant biological barriers. Unlike other members of the Ericaceae family, this species shows extreme recalcitrance in ex situ propagation, linked to deep physiological dormancy in seeds and a low capacity to respond to exogenous growth regulators in asexual propagules (Luteyn & Pedraza-Peñalosa, 2013). Furthermore, the high genetic variability observed in natural populations in the Ecuadorian Andes complicates the standardization of propagation protocols, as different genotypes may respond differently to in vitro conditions (Vega-Polo et al., 2020).

Recent studies suggest that the success of establishing V. floribundum outside its natural habitat does not depend solely on the propagation method, but on the complex interaction between the plant genotype and soil microbial communities. The dependence of this species on specific fungal symbiosis in the páramo largely explains the recurrent failures when using sterile commercial substrates or peat (Ramirez-Villacis et al., 2023a).

Despite its ecological importance, standardized ex situ propagation protocols for wild V. floribundum are lacking, representing a critical bottleneck for its domestication and conservation. The objective of this study was to evaluate the ecological and biological barriers limiting both sexual and asexual propagation of V. floribundum under standard nursery conditions. We hypothesized that (1) standard cold stratification is insufficient to overcome the deep physiological dormancy of wild seeds, and (2) the rhizogenic success of asexual propagules is strictly dependent on the interaction between exogenous hormonal stimulation (IBA) and the presence of native paramo soil microbiomes. By identifying these specific bottlenecks, this study aims to provide a scientific baseline for developing advanced biotechnological protocols for the species.

## 2. MATERIALS AND METHODS

### 2.1. Study Area and Plant Material Source

This study was conducted at the Forest Nursery of the Higher Polytechnic School of Chimborazo (Riobamba, Ecuador; 01°40′S, 78°41′W, 2,780 masl.). All plant materials (seeds and rhizomes) were wild-harvested from the "Mindala Loma" sector within the Chimborazo Faunal Production Reserve (01°27′45″S, 78°56′05″W, 4,261 mals). Ecologically, the collection site is characterized by herbaceous paramo vegetation and sandy loam soils with low organic matter content (0.90%) and acidic pH (5.27) (Caranqui-Aldaz et al., 2022) (Figure 1).

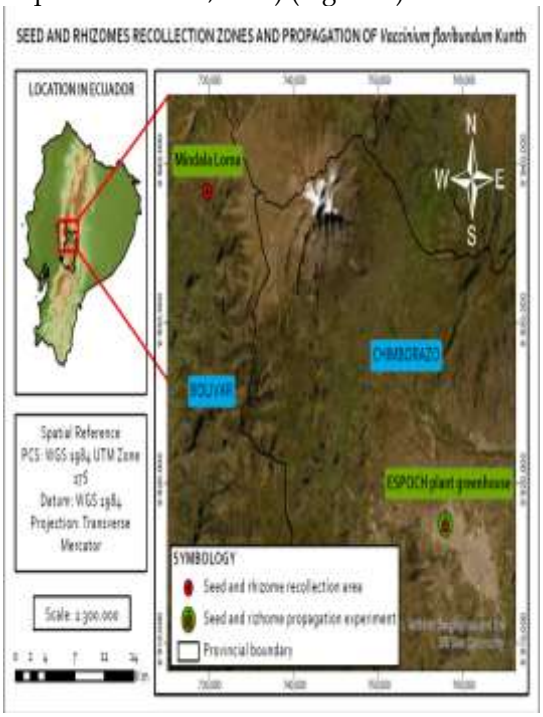


***Figure 1. Location of "Mindala Loma" site for the collection of seed and rhizome of V. floribundum Kunth.***

### 2.2. Experimental Design

To evaluate the asexual propagation bottlenecks, the experiment was structured under a Completely Randomized Design (CRD) with a 23 factorial arrangement. The three evaluated factors (each at two levels) were: substrate type (S1: Native paramo soil vs. S2: Canadian peat), rhizome thickness (>1 cm vs. <1 cm), and exogenous hormonal stimulation (400 mg $L^{-1}$ of IBA vs. 0 mg $L^{-1}$). The experimental unit consisted of 12 rhizomes per treatment combination.

### 2.3. Seed Extraction and Physical Selection

Mature berries (dark purple/black) were harvested during the rainy season (March). No external fungicidal or sanitizing treatments were applied to the seeds. To simulate natural cold stratification, seeds were refrigerated for one month at a constant temperature of 3 °C. Prior to sowing, seed viability was indirectly ensured using the buoyancy method; only high-density seeds that sank in distilled water (indicating a fully developed endosperm and intact embryo) were selected for the trials. Floating seeds were discarded as empty or malformed. A stereomicroscopic inspection was additionally performed to exclude seeds with mechanical damage.

### 2.4. Rhizome Preparation and Substrate Establishment

Rhizomes were excavated in October and uniformly trimmed to 5 cm segments, ensuring the presence of at least two viable buds per propagule. No prophylactic fungicide was applied prior to planting. For hormonal treatments, an indole-3-butyric acid (IBA) solution (400 mg $L^{-1}$) was prepared (diluted with 1N NaOH and distilled water). Assigned rhizomes were immersed in the IBA solution for five minutes prior to planting. The rhizomes were planted horizontally at a depth of 2 cm in propagation beds measuring 4.0 x 1.30 m, utilizing 30% of the available surface area. The beds contained either native paramo soil (S1) or commercial Canadian Sphagnum peat (PRO-MIX®) (S2). Prior to planting, the commercial peat was used in its standard sterile state, while the native paramo soil was covered with black plastic for 24 hours as pre-planting conditioning.

The experiment was maintained under controlled nursery conditions characterized by a mean annual temperature of 20.0 °C and a natural photoperiod of 12 hours. To mitigate initial transplant shock, a shade net providing 20% light attenuation was applied during the establishment phase and subsequently removed once the explants were established. All experimental units received a standardized irrigation volume of 83 mL of pond water (pH ranging from 5.8 to 6.34) per cutting, applied three times a week to consistently maintain the substrates at 80% field capacity.

### 2.5. Data collected

The following propagation parameters were evaluated: Bud presence, shoot length, numbers of pairs of leaves, and the presence or absence of roots. Data were recorded at intervals of 60, 90, 120, 150, and 180 days after planting (Gutiérrez Madrid & Camacho Campos, 2011).

### 2.6. Statistical analysis

Data were analyzed using a randomized 23 factorial design. Prior to formal analysis, the assumptions of normality and homoscedasticity were verified using the Shapiro-Wilk and Levene's tests, respectively. For asexual propagation parameters (survival, shoot length, and number of leaves), a three-way Analysis of Variance (ANOVA) was performed to evaluate the primary effects of provenance, substrate, and IBA concentration, as well as their secondary interactions. When significant differences were detected ($p < 0.05$), a Tukey's Honestly Significant Difference (HSD) post-hoc test was applied for multiple comparisons of means. Due to the absolute null response (0%) observed in all sexual propagation treatments, these data were excluded from the formal ANOVA and were instead analyzed descriptively as evidence of physiological recalcitrance. All statistical procedures and data visualizations (Mean ± SE) were conducted using R software (version 4.3.1) with the stats and ggplot2 packages (R: The R Project for Statistical Computing, n.d.).

Furthermore, a Principal Component Analysis (PCA) was performed using the standardized variables to visually assess the morpho-physiological clustering and multidimensional relationships between the experimental treatments.

## 3. RESULTS

### 3.1. Sexual Propagation

Throughout the evaluation period (60, 90, and 120 days after sowing), seed germination was entirely unsuccessful across all experimental units, resulting in a 0% germination rate. Since standard cold stratification failed to break the dormancy, these data were excluded from further statistical modeling and are treated as qualitative evidence of deep biological recalcitrance.

### 3.2. Asexual Propagation

#### 3.2.1. Substrate Dehydration and Morphological Responses

Although uniform humidity conditions were maintained in the nursery, substrates comprising Canadian peat (S2) exhibited more rapid dehydration compared to the native paramo soil (S1). This variation in moisture retention visibly impacted the early establishment of the rhizomes. Root development at 180 days after planting was exclusively observed in treatments supplemented with 400 mg $L^{-1}$ of IBA and thicker rhizomes (>1 cm), specifically T1 and T5.

#### 3.2.2. Survival and Growth Parameters

The morpho-physiological parameters of the rhizomes were significantly influenced by the interaction of the applied factors (Table 1). The highest survival and growth rates were recorded in T1, which combined native soil (S1), thick rhizomes, and hormonal stimulation.

***Table 1. Effect of substrate, rhizome thickness, and exogenous IBA on the survival and morphological growth parameters of V. floribundum rhizomes at 150 days.***

| Treatment | Substrate | Thickness (cm) | IBA (mg $L^{-1}$) | Survival (%) | Shoot Length (cm) | Leaves (pairs) |
|---|---|---|---|---|---|---|
| **T1** | S1 | > 1 | 400 | 25.0 ± 2.1 a | 10.0 ± 0.5 a | 10.0 ± 0.8 a |
| **T2** | S1 | > 1 | 0 | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.0 ± 0.0 b |
| **T3** | S1 | < 1 | 400 | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.0 ± 0.0 b |
| **T4** | S1 | < 1 | 0 | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.0 ± 0.0 b |
| **T5** | S2 | > 1 | 400 | 16.6 ± 1.8 a | 8.0 ± 0.4 a | 10.0 ± 0.6 a |
| **T6** | S2 | > 1 | 0 | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.0 ± 0.0 b |
| **T7** | S2 | < 1 | 400 | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.0 ± 0.0 b |
| **T8** | S2 | < 1 | 0 | 0.0 ± 0.0 b | 0.0 ± 0.0 b | 0.0 ± 0.0 b |
| **ANOVA** | | | | | | |
| Substrate | | | | *** | ** | ** |
| Thickness | | | | *** | *** | *** |
| IBA | | | | *** | *** | *** |

***Note: S1 = Paramo soil; S2 = Canadian peat. Data are presented as Mean ± SE. Values followed by different letters within the same column indicate significant differences according to Tukey's HSD test ($p < 0.05$). Significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.***

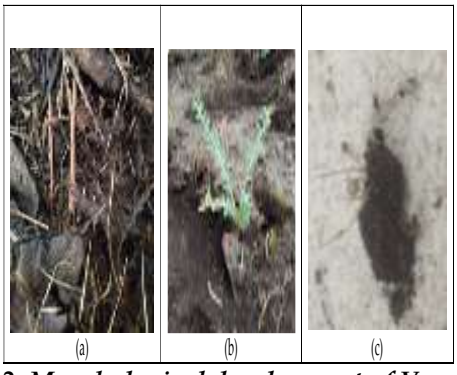


***Figure 2. Morphological development of V. floribundum rhizomes: (a) shoot bud formation, (b) leaf expansion, and (c) root development.***

### *3.2.3. Factorial Interactions*

The three-way ANOVA revealed significant interactions between the substrate and IBA concentration ($p < 0.05$). Specifically, the rhizogenic efficacy of 400 mg $L^{-1}$ of IBA was significantly modulated by the type of substrate used; the highest morpho-physiological response and shoot development were recorded when the hormone was applied in combination with native paramo soil (T1). This synergistic effect suggests that the physicochemical properties or the microbial load of the native soil (S1) may facilitate the metabolic uptake and signaling of exogenous auxins better than the sterile commercial peat (S2). In contrast, the interaction between provenance and IBA was not significant ($p > 0.05$), indicating that the recalcitrant response to hormonal treatment is a consistent trait across the studied populations in the Chimborazo Reserve, regardless of their geographical origin.

### *3.2.4. Principal Component Analysis (PCA)*

To further elucidate the morpho-physiological divergence among the applied treatments, a Principal Component Analysis (PCA) was performed on the evaluated parameters (Figure 3). The first two principal components (PC1 and PC2) accounted for 84.6% of the total cumulative variance. PC1 (55.9%) was primarily driven by the proliferation of cauline and foliar buds, as well as shoot length, distinctly separating the highly responsive Treatment 1 (native paramo soil, >1 cm thickness, 400 mg $L^{-1}$ IBA) from the non-responsive treatments (T2–T4, T6–T8). Meanwhile, PC2 (28.7%) highlighted the variance associated with root development and leaf pairing, illustrating a distinct physiological cluster for Treatment 5 (Canadian peat). This multivariate distribution visually confirms the synergistic efficacy of the native microbiota combined with exogenous auxins, demonstrating that the establishment bottlenecks are overcome by specific, multidimensional morpho-physiological responses.

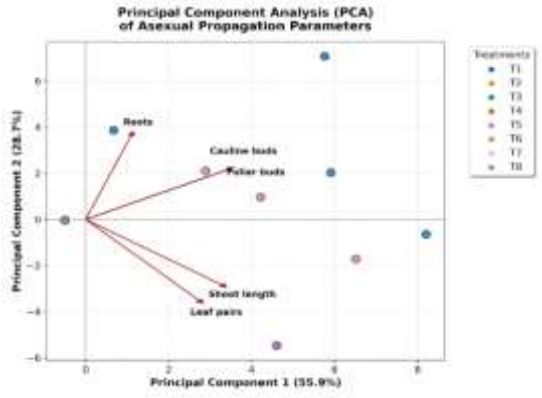


***Figure 3. Principal Component Analysis (PCA)*** biplot displaying the clustering of V. floribundum asexual propagation treatments based on morpho-physiological parameters. Vectors (red arrows) indicate the direction and magnitude of the variables driving the principal components (S1: Paramo soil; S2: Canadian peat).

## 4. DISCUSSION

The complete absence of germination (0%) observed across all provenances under standard cold stratification does not imply that sexual reproduction is biologically unviable, but rather underscores the extreme deep physiological dormancy characteristic of wild V. floribundum populations. This behavior is consistent with the findings of Vega-Polo et al. (Vega-Polo et al., 2020), who noted that wild Andean genotypes have evolved to delay germination until specific environmental cues from their niche are met. In high-altitude ecosystems like the paramo, seed dormancy is a crucial evolutionary adaptation to avoid lethal freezing temperatures and ensure seedling emergence only during favorable seasonal windows (Llivisaca-Contreras et al., 2022). According to Finch-Savage & Leubner-Metzger (2006), breaking deep physiological dormancy in wild montane species requires complex interactions between diurnal temperature fluctuations and prolonged stratification. Furthermore, ecological literature suggests that natural germination in neotropical Ericaceae is closely linked to endozoochory passage through the digestive tract of native birds or mammals which provides crucial chemical scarification (Baskin & Baskin, 2014). Our results empirically demonstrate that standard nursery pre-treatments (cold stratification alone) are entirely insufficient. Consequently, future domestication protocols must mandate the use of acid scarification, gibberellic acid (GA3) priming, or simulated gut transit to overcome these evolutionary tegumentary barriers (Magnitskiy et al., 2011).

Importantly, this null response cannot be attributed to initial seed inviability, as a rigorous physical selection process (buoyancy and morphological inspection) was implemented prior to sowing to ensure the presence of consistent endosperms (Baskin & Baskin, 2014). Our results empirically demonstrate that standard nursery pre-treatments (cold stratification alone) are entirely insufficient to break this seed coat and physiological dormancy. While some studies report varying degrees of success with related species, our findings confirm that for wild mortiño in the Chimborazo region, future domestication efforts must

mandatorily incorporate advanced chemical scarification or acid treatments to simulate natural gut transit and overcome this evolutionary barrier.

A fundamental finding of this study was the superior performance of native paramo soil compared to Canadian peat. While peat is a global horticultural standard for commercial Vaccinium cultivation due to its high porosity and low pH (Blythe et al., 2007), it acted as an abiotic stressor for this wild species. The low survival rates in peat-based substrates (T5–T8) align with the findings of Ramirez-Villacis et al., (2023) who demonstrated that the rhizosphere of V. floribundum depends on highly specific fungal and bacterial assemblies. The roots of Ericaceae naturally form ericoid mycorrhizae (ErM), a specialized symbiotic relationship essential for nitrogen and phosphorus acquisition in highly organic, nutrient-poor, and acidic highland soils (READ, 1996). As demonstrated by Bizabani & Dames (2015) and Caspersen et al. (2016), the absence of these native ErM inoculums in sterile commercial substrates directly inhibits metabolic nutrient uptake, severely reducing post-transplant survival and stress resistance in Vaccinium species. Therefore, successful domestication must move beyond traditional sterile media and integrate native soil inoculums or isolated ErM strains to maximize nursery establishment (Scagel, 2005).

Regarding exogenous hormonal stimulation, the selection of a single IBA concentration (400 mg $L^{-1}$) was based on preliminary nursery constraints and standard baseline protocols often applied to related Andean species like V. meridionale (Ramirez-Villacis et al., 2023b). Although indole-3-butyric acid (IBA) is a standard auxin known to promote adventitious root formation by regulating cell division and elongation ( Steffens & Rasmussen, 2016; Lakehal & Bellini, 2019). The limited overall response indicates a high degree of ontogenetic recalcitrance in mature V. floribundum tissues. The synergistic effect observed when IBA was combined with native soil suggests that the paramo microbiome may facilitate the enzymatic degradation of the rhizome epidermis or assist in auxin signaling pathways (de Klerk et al., 1999; Overvoorde et al., 2010). While exploring a wider dose range or alternative auxin application methods is a necessary avenue for future research (Blythe et al., 2007), the superior survival of rhizomes thicker than 1 cm provides a practical baseline. This is likely due to the greater starch and carbohydrate reserves required to sustain the explant during the prolonged, energy-demanding process of adventitious root formation (Ahkami et al., 2009; Druege et al., 2019).

Our findings redefine the challenges of V. floribundum domestication. Rather than a methodological failure, the low germination and survival rates provide empirical evidence of the species' high niche specificity and recalcitrance. Future efforts must transition from traditional horticultural protocols toward a biotechnological approach that integrates mycorrhizal inoculation and advanced dormancy-breaking treatments to overcome these biological bottlenecks.

While vegetative propagation is influenced by multiple phenological factors, such as the exact age of the mother plant or specific harvest seasonality, our experimental design specifically aimed to address the most urgent bottlenecks faced by local conservation stakeholders: substrate constraints and hormonal recalcitrance. These are the foundational steps required before optimizing chronobiological variables in future studies.

## 5. CONCLUSIONS

The domestication of wild Vaccinium floribundum is significantly hindered by deep physiological and biological recalcitrance. Sexual propagation is severely limited by deep seed dormancy; standard cold stratification is entirely insufficient to trigger germination, indicating that future protocols must incorporate complex ecological simulations, such as acid scarification or endozoochory. Asexually, propagation success is strictly dependent on the synergistic interaction between native paramo soil and exogenous hormonal stimulation (IBA) on mature rhizomes (>1 cm thick). Commercial sterile substrates, such as Canadian peat, act as abiotic stressors and fail to support plant establishment. Consequently, successful ex situ conservation and commercial propagation programs for this species must shift away from standard horticultural practices and prioritize the emulation of native edaphic conditions and advanced dormancy-breaking biotechnologies. Consequently, overcoming these biological bottlenecks is the critical first step toward the sustainable agricultural production, nursery management, and commercial domestication of wild V. floribundum.

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