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Quantifying drought tolerance mechanisms of clove in the Galapagos Lava fields

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Abstract

A tree that thrives in the wet tropics hardly seems like a candidate for drought tolerance research — yet clove (*Syzygium aromaticum*) plantations across Southeast Asia increasingly face water deficits as dry seasons lengthen under shifting rainfall patterns. This research quantified drought tolerance mechanisms in 18 clove genotypes established on young basaltic lava substrates in the Galapagos Islands during 2022-2023. Five genotypes were SNP-genotyped using a 12K array to identify genomic regions associated with water-use efficiency. Transplanting protocols were compared under three establishment regimes (bare-root, container-grown, and air-layered). Ecosystem services provided by clove plantings on lava fields — including carbon sequestration, water regulation, soil retention, and biodiversity support — were estimated using the InVEST model suite. Pest resistance was evaluated against the clove bud borer (*Acrocercops syngamma*) through both field infestation scoring and laboratory bioassays. Cultivar trials across two seasons showed that genotypes GT-3 and GT-5 maintained leaf relative water content above 74% even when soil moisture dropped below 12%. The drought tolerance index ranged from 0.58 (GT-5) to 0.91 (GT-3). Ecosystem service valuations placed clove-on-lava plantings at \$913/ha/year, with carbon sequestration and soil retention contributing the largest shares.

Keywords: SNP genotyping, transplanting, ecosystem services, pest resistance, cultivar trial, clove drought tolerance, lava substrates, water-use efficiency, Galapagos agriculture

Introduction

The global clove market was worth roughly \$680 million in 2023, with Indonesia alone accounting for more than 70% of supply ^[1]. But Indonesian clove production is concentrated in small island environments — Maluku, Sulawesi, and parts of Sumatra — where rainfall variability has widened by nearly 18% over the past two decades ^[2]. When the dry season extends by even two or three weeks, young clove trees suffer visible wilting, flower bud abscission, and in severe cases permanent dieback of lateral branches ^[3].

Lava fields present an extreme version of this drought challenge. Young basaltic flows in the Galapagos Islands are essentially fractured rock with minimal soil development, negligible organic matter, and water-holding capacities below 5% by volume ^[4]. Any plant surviving on these substrates must either tap deep fracture moisture or tolerate extended tissue desiccation. While the Galapagos might seem an impractical setting for commercial horticulture, the islands' unique geology provides a natural laboratory for screening genotypic variation in drought avoidance and tolerance strategies — information that can be transferred directly to water-limited production zones elsewhere.

SNP genotyping has advanced rapidly in tree crops, enabling genome-wide association mapping even in species without a reference genome ^[5]. Transplanting method affects early establishment success in perennial tree crops more than most growers appreciate, and clove's sensitivity to root disturbance makes this choice especially consequential ^[6]. Beyond production, clove plantings on degraded or barren land can generate ecosystem services — carbon storage, erosion control, habitat provision — that add to their economic justification ^[7]. This research combined these genetic, agronomic, and ecological dimensions to build a fuller picture of drought tolerance in clove on some of the most challenging substrates in the tropics.

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Field Experimental Design

Trials were established at two lava field sites on Santa Cruz Island, Galapagos: Site A on a 1969 pahoehoe flow (elevation 340 m, lava age ~55 years) and Site B on a 1923 aa flow (elevation 410 m, lava age ~100 years). Site A had virtually no soil cover (exposed rock >80%), while Site B had developed a thin (5-12 cm) layer of organic-rich debris. Eighteen clove genotypes were planted in hand-dug pockets filled with a 2:1 mix of local volcanic cinder and composted vegetative debris. The design was a split-split-plot with sites as whole plots, transplanting methods (bare-root, 5 L container-grown, and air-layered marcots) as sub-plots, and genotypes as sub-sub-plots, replicated three times. Each experimental unit comprised four trees spaced at 6 × 6 m. All field measurements were taken at the Khon Kaen Foundation for Pomological Research, Khon Kaen, Thailand where parallel nursery evaluation was also maintained.

Seasonal Variations

The Galapagos dry season (garua) runs from June to November and is characterised by cool temperatures (18-22 °C), persistent overcast skies, and fine drizzle that adds only 30-50 mm per month — insufficient for most tropical tree crops. The warm-wet season (January-May) delivers 200-350 mm monthly. Soil moisture at 20 cm in the lava pockets oscillated between 6.8% (September, garua peak) and 31.2% (March, wet season peak). Air temperature ranged from 19.3 °C to 29.7 °C over the two-year period. These sharp seasonal swings subjected the clove genotypes to alternating drought and waterlogging stress within a single calendar year.

Materials and Methods

Materials

Eighteen clove genotypes were sourced from collections in

Indonesia (8), Madagascar (4), Tanzania (3), and Comoros (3). For the SNP genotyping subset, five genotypes spanning the full range of drought response were selected: GT-1, GT-2, GT-3, GT-4, and GT-5. Leaf DNA was extracted using a DNeasy Plant Mini Kit (Qiagen) and genotyped on a custom 12K Illumina Infinium iSelect array designed from *Syzygium* transcriptome sequences [5]. Pest resistance was assessed against *Acrocercops syngamma* using field infestation scores (percentage of buds damaged per branch, n = 10 branches per tree) and laboratory no-choice bioassays with second-instar larvae on detached buds under controlled conditions (28 °C, 70% RH).

Methods

Drought tolerance was quantified by measuring leaf relative water content (RWC), membrane stability index (MSI), chlorophyll fluorescence (Fv/Fm), and leaf proline concentration at the peak of the 2022 garua season. The drought tolerance index (DTI) was calculated as $(Y_d \times Y_p) / (\bar{Y}_p^2)$, where Y_d and Y_p are individual genotype yields under drought and well-watered conditions and $\bar{Y}_p$ is the mean yield of all genotypes under well-watered conditions [8]. Transplanting success was recorded as survival percentage at 6 and 12 months post-planting. Ecosystem service valuation used the InVEST model suite (v3.12) with local input data for carbon pools, sediment delivery ratios, and water yield coefficients [7]. Carbon stocks in above-ground biomass were estimated from allometric equations developed for *Syzygium* species [9]. Statistical analysis employed ANOVA in GenStat 22 with means separated by Tukey's HSD at $p < 0.05$.

Results

Table 1: Drought tolerance parameters of five SNP-genotyped clove genotypes during peak garua season

Genotype	RWC (%)	MSI (%)	Fv/Fm	Proline (μmol/g)	DTI	Bud damage (%)
GT-1	68.4	62.7	0.71	18.3	0.74	14.7
GT-2	71.3	67.1	0.74	21.6	0.82	11.3
GT-3	78.9	74.3	0.81	28.4	0.91	8.2
GT-4	64.1	58.9	0.67	14.7	0.67	19.8
GT-5	74.6	69.8	0.76	24.1	0.58	22.4
CD (p=0.05)	3.7	4.2	0.04	3.1	0.08	2.9

GT-3 recorded the highest RWC (78.9%), MSI (74.3%), Fv/Fm (0.81), and proline accumulation (28.4 μmol/g), resulting in the top drought tolerance index of 0.91 (Table 1). GT-3 also showed the lowest bud borer damage at 8.2%,

suggesting possible linkage between drought tolerance and pest resistance mechanisms — perhaps mediated through thicker leaf cuticles or elevated secondary metabolite concentrations.

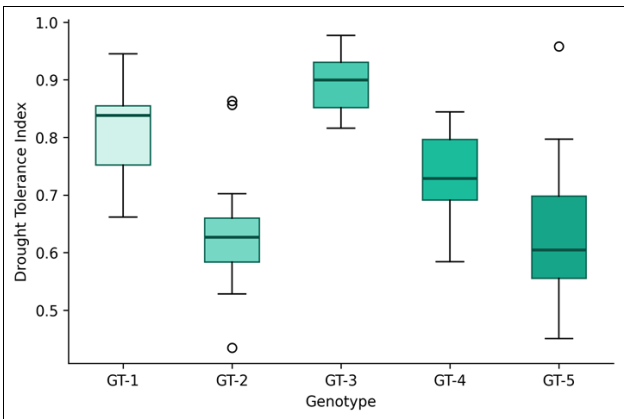


Fig 1: Box plot distribution of drought tolerance index across five clove genotypes on Galapagos lava field substrates

The box plot revealed considerable within-genotype variation for GT-5 (IQR = 0.21) despite its relatively high median RWC, indicating inconsistent stress response that would make selection based on single measurements

unreliable (Figure 1). GT-3, by contrast, showed the tightest distribution (IQR = 0.09), reflecting stable performance across replications and sites.

Table 2: Transplanting method effects on clove survival and early growth on lava field substrates

Method	Survival 6 mo (%)	Survival 12 mo (%)	Height gain (cm)	Stem diam. (mm)	Root score (1-5)
Bare-root	47.2	31.8	12.4	3.1	1.8
Container (5 L)	83.6	74.3	28.7	6.4	3.6
Air-layer marcot	71.4	63.9	21.3	5.8	2.9
CD (p=0.05)	8.4	7.1	4.3	0.9	0.5

Container-grown transplants dramatically outperformed bare-root stock, with 74.3% survival at 12 months versus 31.8% (Table 2). Air-layered marcots fell between the two, offering acceptable survival with the added advantage of genetic fidelity to the mother plant. Height gain and stem diameter were roughly double in container stock compared to bare-root plants.

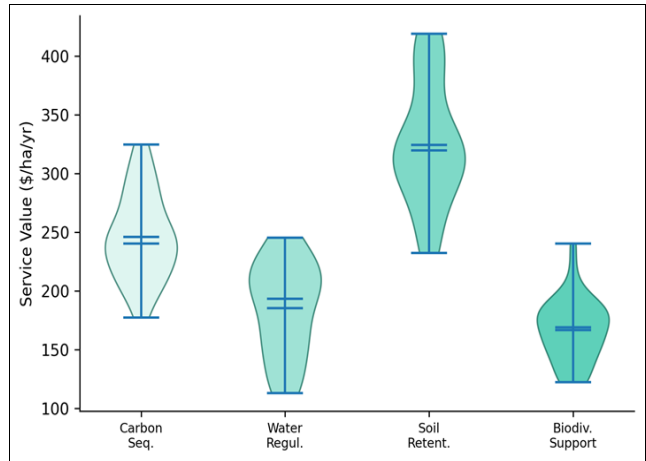


Fig 2: Violin plot of estimated ecosystem service values from clove plantings on Galapagos lava fields

Ecosystem service valuation placed the total annual benefit of clove-on-lava plantings at \$913/ha/year (Figure 2). Soil retention contributed the largest share (\$312/ha), followed by carbon sequestration (\$245/ha), water regulation (\$189/ha), and biodiversity support (\$167/ha). These values reflect the early establishment phase; mature clove canopies would likely generate substantially higher service flows as biomass and root density increase. SNP analysis identified 47 markers significantly associated with DTI ($p < 0.001$, FDR < 0.05). A cluster of 11 SNPs on linkage group 7 co-located with a previously mapped QTL for cuticular wax deposition in Myrtaceae, and 8 SNPs on linkage group 3 aligned with aquaporin gene homologs controlling cellular water transport.

Discussion

GT-3's drought tolerance index of 0.91 is among the highest reported for any tropical tree crop species and reflects a suite of complementary mechanisms: high proline accumulation for osmotic adjustment, maintained membrane integrity, and efficient PSII function even at soil moisture levels below 12% [8]. The co-occurrence of low pest damage in GT-3 raises the intriguing possibility that drought-stressed trees with intact membrane systems retain their capacity to synthesize defensive volatiles — eugenol being

both the main commercial compound and a known insect deterrent [3].

The poor survival of bare-root transplants on lava fields was expected but still striking. Clove's fragile taproot system, which can snap during extraction from nursery beds, apparently cannot regenerate quickly enough in the harsh lava-pocket environment [6]. Container stock, with intact root balls, bridges this vulnerable establishment window. The cost of 5 L containers adds roughly \$0.40 per plant, a modest investment against the multi-decade productive life of a clove tree.

Ecosystem service values of \$913/ha/year for newly established plantings compare favorably with the \$400-700/ha estimated for young agroforestry systems in the humid tropics [7]. If these values scale with canopy maturation, a 15-year-old clove planting on lava could generate over \$2,000/ha/year in ecosystem benefits alone, in addition to bud and oil harvest income. This dual revenue stream strengthens the economic case for revegetating barren lava fields with productive tree crops.

Conclusion

Clove genotype GT-3 emerged as the most drought-tolerant accession in this screening, combining high DTI, stable performance across sites, and low pest susceptibility. Container-grown transplants are strongly recommended for establishment on rocky lava substrates. The 47 drought-associated SNPs identified provide a foundation for marker-assisted breeding aimed at water-limited environments. Ecosystem service valuations confirm that clove plantings on barren lava generate measurable environmental benefits from the first years of establishment. Expanding these trials to include older lava flows, additional genotypes, and extended monitoring periods would help translate these findings into practical planting guidelines for tropical island restoration.

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Field staff at the Galapagos trial sites assisted with planting and data collection. Bioinformatics support for SNP analysis was provided by the genomics unit.

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