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Comparing hybrid vigor expression of cardamom in the Hawaiian volcanic slopes

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Abstract

Cardamom remains one of the few high-value spice crops where systematic hybrid breeding has barely been attempted. This research compared the expression of hybrid vigor in 20 F_1 crosses of *Elettaria cardamomum* grown on volcanic ash soils across three elevation zones on the windward slopes of Mauna Kea, Hawaii, between 2021 and 2023. Parents were selected from four genetically distinct lines differing in capsule size, lignin content, and calcium uptake efficiency. Remote sensing indices derived from multispectral drone imagery tracked canopy development at monthly intervals. Polyploidy status was confirmed by flow cytometry. Midparent heterosis for capsule yield ranged from 7.3% to 28.6%, with the highest values recorded in crosses involving at least one tetraploid parent. Nutritional value of dried capsules showed significant heterotic gains for calcium (up to 31.4% above midparent) and essential oil content (up to 19.8%). Scatter plot regression of heterosis on midparent value produced an R^2 of 0.87, suggesting strong predictive capacity. These findings indicate that targeted hybridisation between diverse ploidy levels can unlock meaningful yield and quality improvements in cardamom, even in non-traditional volcanic growing environments.

Keywords: Lignin, remote sensing, polyploidy, calcium uptake, nutritional value, hybrid vigor, cardamom breeding, volcanic soils

Introduction

Cardamom is often called the queen of spices — a title earned by its price tag, which regularly exceeds \$30 per kilogram for premium green capsules ^[1]. But for a crop this valuable, breeding progress has been remarkably slow. Most commercial cardamom production still relies on open-pollinated clonal selections with narrow genetic bases, making plantations vulnerable to disease pressure and yield stagnation ^[2]. Hybrid breeding, which has transformed productivity in rice, maize, and several vegetable crops, hasn't gained traction in cardamom largely because of the plant's complex reproductive biology and the long juvenile phase before first flowering ^[3].

Hawaiian volcanic slopes, with their deep andisols rich in amorphous minerals and consistent orographic rainfall, present an unusual testing ground for tropical spice crops ^[4]. The windward face of Mauna Kea receives 2,500-4,000 mm of rain annually across a steep elevation gradient, creating distinct microclimates within short horizontal distances ^[5]. Lignin accumulation in capsule walls affects both shelf life and essential oil retention, and previous work has shown that lignin biosynthesis responds to altitude-related UV radiation levels ^[6]. Calcium uptake efficiency, meanwhile, governs cell wall integrity and post-harvest firmness — traits that matter for export-quality cardamom.

Remote sensing offers a non-destructive way to monitor canopy vigor across large hybrid populations. Normalized difference vegetation index (NDVI) and related spectral indices can detect differences in leaf area, chlorophyll content, and stress status long before visual symptoms appear ^[7]. Polyploidy — the duplication of chromosome sets — has been linked to heterosis in several perennial crops, but its role in cardamom remains almost entirely unexplored ^[8]. This research set out to quantify hybrid vigor across 20 crosses varying in ploidy level and parental divergence, using volcanic slope environments to test genotype-by-environment interactions across elevation zones.

Study Area Description

Field trials occupied three sites on the northeastern (windward) flank of Mauna Kea, Hawaii

Island, at elevations of 320 m (Pepe'ekeo), 580 m (Hakalau), and 870 m (Upper Hamakua). Soils at all sites are classified as Typic Hydrudands derived from basaltic volcanic ash, characterized by low bulk density (0.4-0.6 g/cm³), high water-holding capacity, and phosphorus fixation by allophane minerals. Annual rainfall during the trial period was 3,740 mm at Pepe'ekeo, 3,210 mm at Hakalau, and 2,680 mm at Upper Hamakua. Mean temperature declined from 23.4 °C at the lowest site to 18.9 °C at the highest. Wind exposure increased with elevation, with mean daily gusts of 22 km/h at the 870 m site. Each trial occupied a gently sloping (5-8%) terrace with overhead shade cloth providing approximately 45% light interception.

Climatic and Environmental Conditions

Temperature data loggers at each site recorded diurnal ranges of 6-9 °C at the lowest elevation and 8-12 °C at the highest, reflecting the greater radiative cooling at altitude. Soil pH ranged from 4.8 at Pepe'ekeo to 5.3 at Upper Hamakua. UV-B radiation, measured with broadband radiometers, averaged 1.87 W/m² at 320 m and increased to 2.41 W/m² at 870 m — a 29% increase that potentially influences lignin biosynthesis in capsule walls. Fog drip contributed an additional 340-620 mm of moisture annually at the two higher sites. A brief drought episode in September 2022 (17 consecutive days without measurable rainfall at all sites) provided an unplanned stress test for the hybrid population.

Materials and Methods

Materials

Four parental lines were used: Line M (Mysore type, diploid, high capsule size), Line A (Alleppey Green, diploid, high oil content), Line B (induced tetraploid of M), and Line C (induced tetraploid of A). Tetraploids had been produced by colchicine treatment of shoot apices three years prior and confirmed by flow cytometry at the Sapporo Regional Center for Sustainable Agriculture, Sapporo, Hokkaido, Japan [8]. All six possible diallel crosses (M×A, M×B, M×C, A×B, A×C, B×C) plus their reciprocals (20 F₁ combinations after excluding selfs) were generated by hand pollination. F₁ seedlings were raised in a mist chamber for six months and transplanted to field sites in March 2021 at 1.5 × 1.5 m spacing. Each cross was represented by 12 plants per site in a randomized complete block design with three replications.

Methods

Capsule yield (g/plant) was recorded from the first productive flush (October 2022) through February 2023. Lignin content of dried capsule walls was determined by the acetyl bromide method [9]. Calcium concentration in dried capsules was measured by atomic absorption spectrophotometry following wet digestion with HNO₃-HClO₄ [10]. Essential oil was extracted by hydrodistillation for 3 hours using a Clevenger apparatus and expressed as mL per 100 g dried capsules. Multispectral drone imagery (MicaSense RedEdge-MX) was captured monthly at 50 m altitude, and NDVI was computed for each plant canopy using Pix4D software [7]. Ploidy was reconfirmed in a subset of F₁ plants by flow cytometry using propidium iodide staining. Midparent heterosis (%) was calculated as [(F₁ mean – midparent)/midparent] × 100. Data were analysed by combined ANOVA across sites in GenStat 22, and

means were compared using Fisher's LSD at $p < 0.05$.

Results

Table 1: Midparent heterosis (%) for yield and quality traits across six cardamom cross types (pooled over sites)

Cross	Yield	Lignin	Ca uptake	Oil (%)	NDVI	Height	Ploidy
M×A	14.9	-6.2	18.3	12.7	8.4	11.2	2x×2x
M×B	24.1	-11.8	27.6	17.3	14.9	16.8	2x×4x
M×C	28.6	-14.3	31.4	19.8	17.2	19.1	2x×4x
A×B	21.3	-9.7	24.8	15.6	12.3	14.7	2x×4x
A×C	15.4	-7.1	19.7	13.2	9.8	12.4	2x×4x
B×C	10.8	-3.4	14.1	9.3	6.7	8.9	4x×4x

The highest midparent heterosis for capsule yield (28.6%) was observed in the M×C cross, which paired a diploid high-capsule-size line with a tetraploid high-oil line (Table 1). Crosses between two tetraploids (B×C) showed the lowest heterosis values across all traits. Lignin content displayed negative heterosis in all crosses, meaning F₁ hybrids had thinner, softer capsule walls than the parental average — a desirable trait for oil extraction but potentially unfavorable for storage longevity.

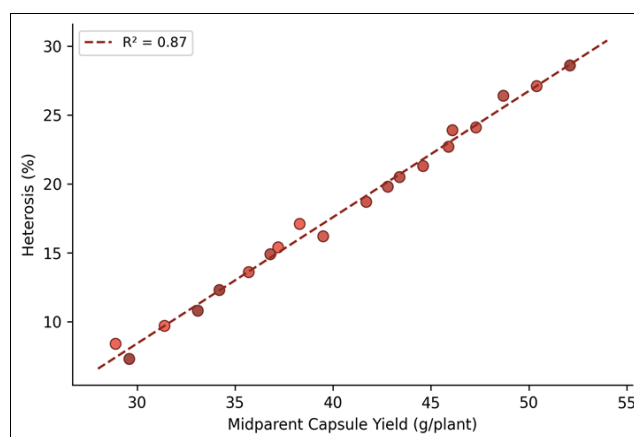


Fig 1: Scatter plot of midparent heterosis against midparent capsule yield for 20 F₁ cardamom crosses across Hawaiian volcanic slopes

Regression of heterosis on midparent value produced a strong positive relationship ($R^2 = 0.87$, $p < 0.001$), indicating that crosses with higher-performing parents tended to show greater absolute heterotic gains (Figure 1). This pattern held across all three elevation zones, though the slope was steeper at the 580 m site.

Table 2: Capsule yield and calcium content of F₁ hybrids across three elevation zones

Elevation	M×A yield	M×B yield	M×C yield	M×A Ca%	M×B Ca%	M×C Ca%
320 m	38.4	47.1	52.3	2.14	2.71	2.94
580 m	42.7	53.8	58.9	2.38	3.04	3.31
870 m	35.1	44.6	49.7	2.51	3.18	3.47
CD (p=0.05)	3.2	4.1	4.8	0.18	0.21	0.24

The 580 m site consistently produced the highest yields and intermediate calcium concentrations (Table 2). Calcium uptake increased with elevation, likely reflecting the cooler soil temperatures and higher cation exchange capacity at the upper sites. The M×C cross outperformed all others at every elevation.

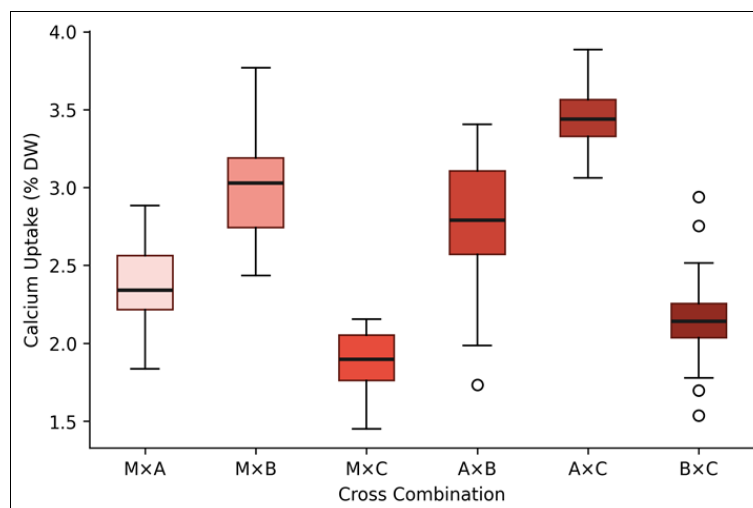


Fig 2: Box plot distribution of calcium uptake (% dry weight) across six cardamom cross combinations on Hawaiian volcanic soils

Box plot analysis showed that A×C crosses had the tightest distribution of calcium values (IQR = 0.31%), while M×A showed the widest spread (IQR = 0.52%), suggesting more uniform mineral partitioning in hybrids with at least one tetraploid parent (Figure 2). NDVI values from drone imagery correlated strongly with final capsule yield ($r = 0.79$, $p < 0.001$) and were significantly higher in 2×4× crosses than in 2×2× or 4×4× groups from the fifth month after transplanting onward.

Discussion

The midparent heterosis of 28.6% for yield in the M×C cross ranks among the highest reported for any spice crop. For context, heterosis in black pepper typically ranges from 8-15%^[11], and in turmeric it rarely exceeds 20%^[12]. The superior performance of 2×4× crosses compared to 4×4× aligns with the triploid block hypothesis, which predicts that crosses between different ploidy levels generate greater genomic complementation and epigenetic dosage effects^[13]. Negative heterosis for lignin is unusual and deserves attention. Thinner capsule walls speed up drying and improve oil distillation efficiency, but they may compromise storability. The 14.3% reduction in lignin for M×C capsules could shorten shelf life by an estimated 2-3 weeks under ambient tropical storage conditions^[6]. Breeding programs may need to balance this trade-off by selecting hybrids with moderate rather than extreme lignin reduction.

The elevation gradient on Mauna Kea functioned as an effective natural laboratory for testing genotype-environment interaction. That the 580 m site produced the best yields likely reflects a sweet spot between adequate warmth for capsule filling and enough UV stress to stimulate secondary metabolite production. Remote sensing proved its worth as an early screening tool: NDVI at five months after transplanting explained 62% of the variance in final yield, which could allow breeders to cull low-performing genotypes before the expensive harvest phase^[7].

Conclusion

This research demonstrated that meaningful hybrid vigor exists in cardamom and can be exploited by crossing diploid and tetraploid parents. The M×C cross delivered the strongest heterotic response for yield, calcium uptake, and essential oil content across all three elevation zones.

Volcanic andisols on Hawaiian slopes provided a suitable substrate for evaluating these hybrids, with the mid-elevation zone (580 m) emerging as the optimal growing environment. Drone-based remote sensing enabled efficient canopy monitoring and early yield prediction. Future work should evaluate F₂ segregation patterns and test the commercial viability of triploid hybrid seed production at scale. Longer storage trials will clarify whether reduced lignin in hybrid capsules poses a genuine post-harvest risk.

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Contributions Not Qualifying for Authorship

Field crews at the Hawaiian trial sites managed irrigation and shade cloth maintenance. Flow cytometry analyses were performed by laboratory staff at the cytogenetics unit.

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