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RESEARCH

Kappaphycus alvarezii cultivars selected using a 'common garden' approach demonstrate improved performance in on-farm trials leading to farmer adoption in Indonesia

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Abstract

A 'common garden' experimental approach was used to evaluate the production and carrageenan properties of *Kappaphycus alvarezii* cultivars collected from ten different locations throughout Indonesia. The evaluation was done with three 45-day culture cycles reproducing the longline cultivation method generally used by Indonesian seaweed farmers. The advantage of the common garden approach is that it isolates genetic variability amongst cultivars by effectively removing the influences of environment and cultivation methods. In the first cycle, four cultivars exhibited high growth rates yielding 146–213 g m^{-1} compared with others which produced only 23–47 g m^{-1}. One cultivar, sourced from Mamuju, was amongst the best performing cultivars in all three cycles and demonstrated consistently high survival of clumps (79–88%). The Mamuju cultivar was subsequently provided to seaweed farmers across South Sulawesi, and its performance compared with that of 'local' cultivars in on-farm trials at three sites (Barru, Jeneponto and Wajo). Production of the Mamuju cultivar in these trials was higher (24–416%) than that of the local cultivars, as was its carrageenan content (up to 32.3% dry weight). The Mamuju cultivar was subsequently adopted by farmers in four locations and, in interviews conducted ~ 5 years later, farmers identified their continued use of the Mamuju cultivar because of its perceived superior growth and morphology. This long-term program of work began with an experimental evaluation of existing cultivars from across Indonesia. We highlight the value of this common garden approach in identifying cultivars with superior performance for provision to commercial seaweed farms.

Keywords Rhodophyta · Carrageenan · *Kappaphycus* · Growth · Genotype · Environment

Introduction

Indonesia is the dominant producer of the carrageenan-yielding seaweeds *Kappaphycus* (colloquially known as 'kotoni') and *Eucheuma* ('spinosum') (Kambey et al. 2020; Langford et al. 2022). Indonesian production in 2023 was estimated at 9.8 million tonnes wet weight and valued at 1.8 billion US$ (MMAF 2025). Seaweed farming provides economic and social benefits to coastal communities that undertake this form of aquaculture (Larson et al. 2021; Rimmer et al. 2021). These benefits are recognised by the Indonesian government which plans the expansion of seaweed farming throughout the archipelago, particularly in Eastern Indonesia where there are limited alternative livelihoods for coastal communities (Rimmer et al. 2021; Langford et al. 2022). Carrageenophyte seaweeds are native to Indonesia, but commercial varieties were introduced from the Philippines and are now widely cultured throughout the archipelago (Ask and Azanza 2002; Neish 2008; Porse and Rudolph 2017). Some local cultivars of *Kappaphycus* may also be cultured, but the origin of most cultivars is now obscure (Neish 2008).

Despite the success of seaweed farming in Indonesia, farmers list a range of challenges, including seasonal variation in production, disease outbreaks, the effects of

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sudden changes in water quality, and limited availability of seedstock. Discussions with farmers in some locations in Indonesia indicate a general trend of decreasing seaweed production, a trend which has also been identified in the Philippines, another major carrageenophyte farming country (Narvarte et al. 2022; Gacura et al. 2026). This decline in productivity and hardiness has been attributed to low genetic variability (Zuccarello et al. 2006), resulting from long-term vegetative reproduction, making many established cultivars more susceptible to environmental stressors, epi- and endophytic pests and diseases such as ice-ice (Porse and Rudolph 2017; Narvarte et al. 2022; Gacura et al. 2026). A recommended response to this issue is develop hardier, faster growing and higher yielding strains with increasing quality of extract through superior post-harvest handling and strain improvement (Ask and Azanza 2002). One line of research has been to evaluate the potential of new 'wild' (i.e. currently uncultivated) strains of *Kappaphycus alvarezii* (Narvarte et al. 2022; Gacura et al. 2026). Another, as described in this paper, is to evaluate and compare *K. alvarezii* cultivars that are already farmed, to identify better-performing commercial cultivars.

In a previous study (Simatupang et al. 2021) we evaluated a range of *K. alvarezii* cultivars from different areas of Indonesia, to examine variation in production and product quality in those cultivars under a standardised culture methodology at 10 different locations across Indonesia. This work identified substantial variability in production (growth and survival) and product quality (carrageenan content, gel strength and viscosity) between the different sites. Production over the 45-day trial period was highly variable, ranging from a high of (mean ± SE) 2819 ± 124 g m^{-1} per rope (Bontang site) to 848 ± 66.7 g m^{-1} to 495 ± 25.2 g m^{-1} for the poorest-performing sites (Mamuju, Gorontalo, Manado and Banten). Carrageenan content of cultured *K. alvarezii* also varied between sites, from 26.4% (Mamuju site) to 8.6–11.7% (Lombok and Bantaeng sites). Gel strength ranged from 735.2 g cm^{-2} (Manado) to 291.5 g cm^{-2} (Bantaeng), and viscosity from 138.8 cP (Lombok) to 30.0 cP (Gorontalo) (Simatupang et al. 2021).

This earlier evaluation (Simatupang et al. 2021) removed one (of three) sources of variability, i.e., different culture methods, and retained two potential sources of variability: genetic variation amongst *K. alvarezii* 'strains' or cultivars (Zuccarello et al. 2006; Lim et al. 2014) and different environmental conditions, particularly temperature and nutrient levels (Muñoz et al. 2004; Kotiya et al. 2011). While the provenance of the seaweed farmed in different locations has not been formally captured, and cytochrome oxidase subunit 1 gene (COI) barcoding shows no diversity in that single marker for farmed *K. alvarezii*, these cultivars have potentially been isolated and propagated for decades, with clear differences in colour, morphology and carrageenan gel phenotypes (Ratnawati et al. 2020; Simatupang et al. 2021) which could have evolved with the selection of fast-growing cultivars (Marshall et al. 2018).

The present study reports a 'common garden' experiment (Rose and Garland 2009) that evaluated seaweed cultivar traits without the confounding effects of different environmental variables associated with different locations (de Villemereuil et al. 2016; Sudatti et al. 2021). A common garden approach effectively removes the second source of variability (different environmental conditions), partitioning genetic variability as the main source of variation observed between cultivars. The best-performing *K. alvarezii* cultivar from this common garden evaluation was subsequently provided to commercial seaweed farmers in South Sulawesi, Indonesia, where its productivity was compared with that of the 'local' cultivar in on-farm trials at three locations. Finally, seaweed farmers were interviewed to better understand their experiences with the selected cultivar ~ 5 years after the completion of the on-farm trials.

Materials and methods

Seaweed sources

Fifty kilogram of cultivated *K. alvarezii* seaweed was collected from each of 10 locations in Indonesia during April – May 2017, as previously described in Simatupang et al. (2021). Details of the locations sampled (including latitude and longitude) are provided in Table 1 and Fig. 1 of Simatupang et al. (2021) and for this study are similarly labelled: Lampung, Banten, Lombok, Kupang, Pangkep, Bantaeng, Mamuju, Gorontalo, Manado and Bontang. Seaweed collected from each location was designated as a 'cultivar' for the purposes of these trials (Simatupang et al. 2021). Photographs of representative samples of each cultivar are shown in Fig. 1.

The samples were transported to the common garden culture site near Boddie Village, Mandalle, Pangkajene dan Kepulauan (Pangkep) District, South Sulawesi (Fig. 2) and acclimated for two weeks prior to commencing the experiment. The Boddie Village location was selected because it had been used as a seaweed trial site, in collaboration with local seaweed farmers, since 2008. Based on this prior experience, the research team was familiar with pest outbreaks, and seasonal fluctuations in growth and production at this site. Additionally, South Sulawesi is relatively central in the Indonesian archipelago, simplifying the collection of

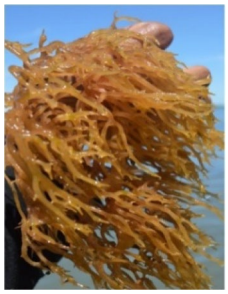
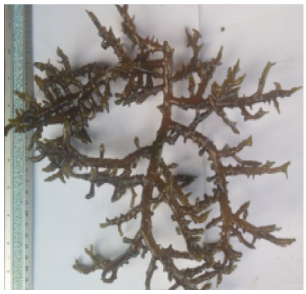
Cultivar	Initial	First cycle	Second cycle
Manado			
Gorontalo			
Mamuju			
Lombok			
Pangkep			

Fig. 1 Representative photographs of the cultivars used in these trials, prior to the commencement of the common garden trial, and following the first and second culture cycles



Fig. 1 (continued)

seaweed cultivars from throughout the archipelago. Furthermore, the site is close (ca. 50 km) to the nationally accredited Ministry of Marine Affairs and Fisheries laboratories at Maros, near Makassar, allowing ease of transport and timely analyses for water quality, seaweed product quality and DNA.

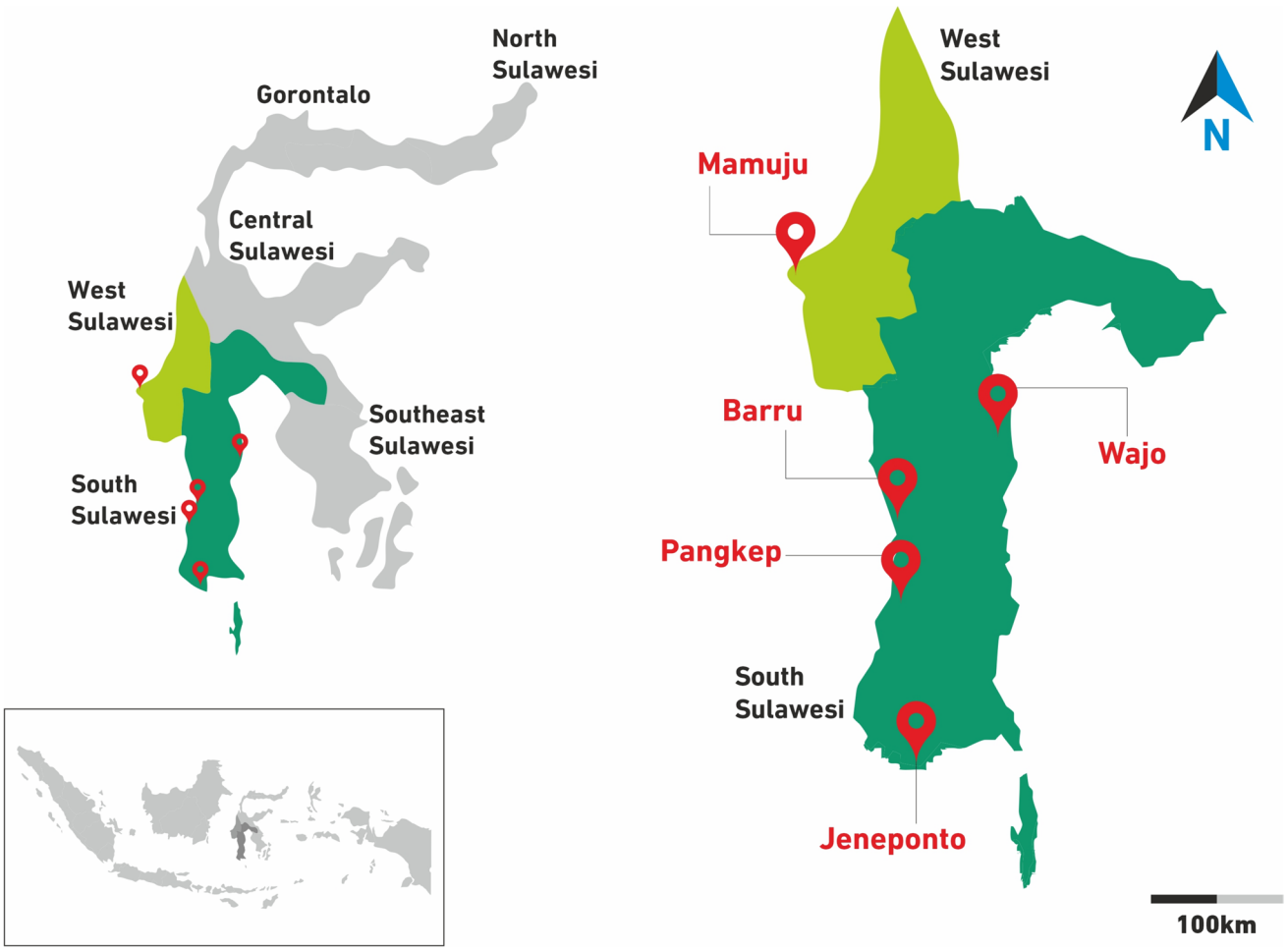


Fig. 2 Location of study area within Indonesia (inset map). Main map (left) of Sulawesi showing Provinces with South Sulawesi Province in dark green and West Sulawesi in light green, showing location of study sites; (right) map of South Sulawesi (dark green) showing location of common garden trial site (Pangkep) and on-farm trial sites (Jeneponto, Barru and Wajo) and Mamuju, West Sulawesi (light green), the source of the cultivar used in the on-farm trials is highlighted

All the samples used in the common garden trials were genetically identified as *K. alvarezii* using the COI marker (Ratnawati et al. 2020), following the methods of Zuccarello and Paul (2019). They were all of an identical COI genotype, corresponding to the main cultivated genotype (Genbank Accession number: KT316556: (Dumilag et al. 2016). Re-sampling of the Mamuju cultivar with new seed collected from Mamuju for the on-farm comparison to local cultivars reaffirmed identical COI sequences (P. Ratnawati, unpublished data).

Experimental design and sampling

The trial was undertaken using the floating longline culture method, with three 45-day cycles using different numbers of *K. alvarezii* cultivars. After transportation to the common garden experimental site, the seaweed cultivars were cultured separately for two weeks to acclimate them to local conditions.

For the first cycle (July–August), three ropes were prepared with seedstock of each cultivar giving a total of 30 ropes (3 ropes × 10 cultivars). For each rope, a total of 230 clumps of seaweed, initial wet weight 50 g per clump, were tied to a 35 m long rope with each clump 15 cm apart shown in Fig. 2 of Simatupang et al. (2021). This equated to an initial stocking density of 330 g m^{-1} (or 11.5 kg per rope). For practical reasons, the three ropes for each cultivar were placed next to each other, with 1 m separation, in this and subsequent cycles. After 45 days of culture all the ropes were harvested, rinsed with seawater, and the total weight (wet weight) of seaweed calculated by subtracting the weight of the rope from the total weight of the rope with seaweed. In addition, the number of surviving clumps per rope was recorded to provide a survival value for each rope.

Following harvest, the best-surviving cultivars were again divided into 50 g clumps and returned to the longlines. For the second cycle (August–October), the cultivars originating from Banten, Gorontalo, Lombok, Mamuju, and Manado were compared. However, due to limited material from the first cycle harvest this second cycle used only two shorter ropes (3 m length) per cultivar with 20 clumps per rope (initial weight of 50 g; equivalent to 330 g m^{-1}). The seaweed was again cultured for 45 days and then harvested.

For the third cycle (October–November), the cultivar that had demonstrated best survival in the previous two cycles (Mamuju cultivar) was cultivated alone to verify its performance in another culture cycle prior to it being distributed to farmers. In this cycle, the Mamuju cultivar was cultured with 230 clumps per rope (50 g per clump, equivalent to 330 g m^{-1}) and three ropes.

At harvest for each of the three cycles, one kilogram of seaweed from each rope (i.e. 3 kg per cultivar) was sun-dried for 2–3 days to approximately 35% moisture content to prepare samples for carrageenan content and gel strength analyses.

Carrageenan content and gel strength

Analysis of the carrageenan content of *K. alvarezii* was done using the potassium hydroxide method (Peranginangin et al. 2013) with some modification. A 250 g sample of sun-dried seaweed was washed three times or until the attached dirt was removed. The sample was heated in 1.5 L of 0.6% KOH solution and water at 60–65 °C for 2 h. The sample was then washed until neutral pH (pH = 7) was obtained, then boiled in water at 90–95 °C for 2 h. The extract was filtered using 100 µm mesh plankton net until gel formation occurred for 1–2 h at room temperature (25–27 °C).

The extract was stored in a freezer at −21 °C for 20 h. The filtrate obtained was further precipitated through the addition of 1.5 L of isopropyl alcohol for 30–60 min. The carrageenan fibre produced was dried in direct sunlight outdoors and then milled using a kitchen blender to obtain carrageenan powder. Carrageenan content was calculated using the following formula:

$$Carrageenan\ content\ (\%) = \frac{Weight\ of\ carrageenan\ fibre\ (g)}{Dry\ weight\ of\ sample\ (g)} \times 100$$

Analysis for gel strength was undertaken using the method of Basmal and Ikasari (2014). This method involved dissolving 1.5 g of dried carrageenan in 100 mL distilled water with 0.5 g KCl. The solution was heated in a bottle (3 cm diameter) to boiling point using a hot plate at 250ºC and a stirrer with a speed of 700 rpm. The solution was then cooled to room temperature (25–27ºC) for 3–4 h, after which the gel strength was measured using a Brookfield CT3 4500 texture analyser. Triplicate samples of each cultivar were measured.

Water quality

Salinity, temperature and pH were measured twice weekly at three locations within each experimental array. Samples for nitrate and phosphate were taken every 30 days. Details of water quality sampling and raw data are provided in the Supplementary Material file.

Farmer grow-out trials

Following the completion of the common garden trial, the best performing cultivar (Mamuju) was compared to locally sourced and cultivated *K. alvarezii* at three locations in Barru, Jeneponto and Wajo districts (Fig. 2). These locations were chosen because they are all significant sites for commercial cultivation of *K. alvarezii*. At each site a longline system was established with three 35 m ropes placed 1 m apart, with the same experimental design as the common garden trial (i.e., 230 clumps of seaweed, initial wet weight 50 g per clump, 15 cm spacing between clumps). Local farmers were employed to manage the experimental cultures, using their normal farming practices.

After 45 days the seaweed was harvested, then washed and weighed as per the protocol for the common garden experiment. Sub-samples of seaweed were dried and later processed for carrageenan content as per the method described above.

Farmer interviews

Following the third experimental culture cycle, the best-performing (Mamuju) cultivar was distributed free of charge by Ministry of Marine Affairs and Fisheries staff to farmers in four districts in South Sulawesi: Pangkep (site of the common garden trial) in 2017 and 2018, and to Barru, Wajo and Jeneponto in 2020. Participating farmers in Pangkep, Barru and Wajo were visited again by Ministry staff in August – September 2024 and surveyed on their personal experience of the performance of the Mamuju cultivar. Farmers were asked about current farming practices; their satisfaction with the Mamuju cultivar; performance of the Mamuju cultivar in comparison to other farmed seaweed cultivars in terms of farm-gate price achieved, growth/production, disease resistance, and performance in different seasons. Stated perceptions of seaweed buyers and other farmers were also elicited from the participants. A total of 30 farmers, ten in each regency, participated in the survey. Nine of the survey participants were women farmers.

Data analyses

Data were analysed using Minitab v17 and SPSS v19 software. Biomass of each rope at harvest, carrageenan content and gel strength data for each cycle were analysed using one-way analysis of variance (ANOVA) after checking homogeneity of variance using Levene's test (Kruskal–Wallis non-parametric test was used as indicated where ANOVA assumptions were not met). We note that the replicate ropes for each cycle are not truly independent replicates as the three ropes for each cultivar were adjacent to each other at the trial site. Where ANOVA indicated significant differences between means ($P < 0.05$), individual means were compared using Fisher's Least Significant Difference (LSD) test (a total of 45 pairwise comparisons between the 10 cultivars). For the farmer trial data, three separate independent t-tests were conducted comparing the Mamuju cultivars to each of the local farmer cultivars (Barru, Jeneponto and Wajo), with a Bonferroni adjustment ($P_{Adj.}$) for multiple comparisons.

Results

Production

For the first cycle, there were significant differences in total weight at harvest between the 10 cultivars evaluated (ANOVA; $F_{9,20} = 7.4$, $P < 0.001$). Four cultivars produced significantly higher biomass than the others: Manado, Gorontalo, Mamuju and Lombok cultivars produced an average of 146–213 g m^{-1} (Table 1). Three cultivars (Bantaeng, Lampung and Kupang) had the lowest biomass at harvest with means of 23–47 g m^{-1} (Table 1). Production by all 10 cultivars was negative for this cycle, and survival (the number of live seaweed clumps) was highly variable, ranging from 87% for the Mamuju cultivar, to a low of 13% for the Kupang cultivar (Table 1). Survival rates were also significantly different (ANOVA; $F_{9,20} = 7.1$, $P < 0.001$) with the Mamuju, Gorontalo and Manado cultivars demonstrating the highest survival (66–87%) (Table 1).

For the second cycle, five cultivars that had performed best in the first cycle (Manado, Gorontalo, Mamuju, Lombok, and Banten) were again evaluated. For this second cycle, there was no significant difference between biomass of the five cultivars evaluated (ANOVA; $F_{4,5} = 0.51$, $P = 0.732$). Growth overall was poor during this cycle with final biomass 76–252 g m^{-1} (Table 1). All five cultivars showed negative growth (down from 330 g m^{-1} initial density) during the second cycle. However, survival in this cycle was higher than for the first cycle with all cultivars demonstrating better than 85% survival (Table 1).

Table 1 Biomass and survival (mean ± SE) at harvest for cultivars of *K. alvarezii* from three 45-day cycles of the common garden experiment

Cycle	Parameter	Cultivar									
		Manado	Gorontalo	Mamuju	Lombok	Pangkep	Banten	Bontang	Bantaeng	Lampung	Kupang
1	Biomass (g m^{-1})	213 ± 40^{a}	$208 \pm 39^{a,b}$	$147 \pm 5^{a,b,c}$	$146 \pm 15^{a,b,c}$	$130 \pm 14^{b,c}$	125 ± 9^{c}	121 ± 49^{c}	47 ± 11^{d}	26 ± 9^{d}	$23 \pm 5d$
($n = 3$)	Survival (%)	$66 \pm 13.4^{a,b,c}$	$70 \pm 12.8^{a,b}$	87 ± 2.0^{a}	$51 \pm 7.6^{b,c}$	$43 \pm 4.6^{b,c,d,e}$	$45 \pm 1.9^{b,c,d}$	$40 \pm 17.4^{c,d,e}$	$21 \pm 6.4^{d,e,f}$	$18 \pm 7.4^{e,f}$	13 ± 2.8^{f}
2	Biomass (g m^{-1})	115 ± 47	167 ± 51	252 ± 98	152 ± 87	-	161 ± 53	-	-	-	-
($n = 2$)	Survival (%)	93 ± 7.5	93 ± 7.5	88 ± 12.5	88 ± 12.5	-	100				
3	Biomass (g m^{-1})	-	-	848 ± 9	-	-	-	-	-	-	-
($n = 3$)	Survival (%)			79 ± 2.8							

Initial density was 330 g m^{-1} for all three cycles. Different superscript letters denote differences between the cultivars (Fisher's LSD, $P < 0.05$). Note replication in Cycle 2 of $n = 2$ ropes due to availability of biomass

For the third cycle, the Mamuju cultivar (which had performed best in the previous two cycles) was cultivated alone to ensure that it would demonstrate positive growth under culture conditions. The results of this third cycle were dramatically different to the second cycle, with the Mamuju cultivar reaching 848 g m^{-1} at harvest with survival of 79% (Table 1). Overall, the Mamuju cultivar was cultured for three cycles, which covered almost half a year of production. Calculating average production for the Mamuju cultivar across the three experimental cycles, the yield was 92 g m^{-1} (45 d cycle)$^{-1}$, equivalent to 746 g m^{-1} y^{-1}. Overall, in the third cycle, there was a 2.6-fold increase in biomass based on the raw data from 330 g m^{-1} to 848 g m^{-1} over 45 days (Table 1). This equates to a specific growth rate (SGR) of 2.1% day^{-1} (calculated from final and initial weights in Table 1, Cycle 3).

Carrageenan content and gel strength

The seaweed cultivars with the highest carrageenan content from the first cycle were from Manado, Gorontalo, Lombok, Pangkep, Mamuju, and Bontang (ANOVA; $F_{9,20}=2.91$, $P=0.022$) with mean carrageenan content ranging from 21.4% down to 17.3% (Table 2). The Lampung, Bantaeng, Kupang, and Banten cultivars showed the lowest carrageenan of the 10 cultivars evaluated in this cycle with means ranging from 15.2% down to 12.0% (Table 2).

Gel strength results showed a different pattern, with the Banten, Bantaeng, Bontang, Lombok and Lampung cultivars having significantly higher gel strength values, ranging from 994 g cm^{-2} down to 813 g cm^{-2}, than the remaining cultivars (ANOVA; $F_{9,20}=4.68$, $P=0.020$). The Manado, Mamuju and Pangkep cultivars had the lowest gel strength values of the 10 cultivars evaluated in this cycle, ranging from 724 g cm^{-2} down to 560 g cm^{-2} (Table 2).

For the second cycle, the average carrageenan content ranged from 7.5% for the Banten cultivar to 19.8% for the Mamuju cultivar (Table 2). Carrageenan content data from this cycle showed unequal variances and data transformations did not improve this, so were analysed using a Kruskal–Wallis non-parametric test which showed significant differences between cultivars ($H_4=13.50$, $P=0.009$). Carrageenan content values for this cycle were generally lower than for the first cycle (12.0–21.4%) (Table 2). Gel strength values for the second cycle ranged from 888–1106 g cm^{-2} (Table 2). There were no significant differences in gel strength between the five cultivars in the second cycle (ANOVA; $F_{4,5}=1.11$, $P=0.404$). For the third cycle, carrageenan content of the Mamuju cultivar was 20.2% and gel strength was 967 g cm^{-2} (Table 2).

Water quality

Water temperature, salinity and pH were relatively stable and remained within the ranges recommended for seaweed

Table 2 Carrageenan content and gel strength data (mean ± SE) for cultivars of *K. alvarezii* from three 45-day cycles of the common garden experiment

Cycle	Parameter	Cultivar									
		Manado	Gorontalo	Mamuju	Lombok	Pangkep	Banten	Bontang	Bantaeng	Lampung	Kupang
1	Carrageenan (%)	21.4 ± 1.1^{a}	20.7 ± 0.9^{a}	$19.2 \pm 1.3^{a,b}$	20.7 ± 0.9^{a}	$19.5 \pm 1.4^{a,b}$	12.0 ± 1.0^{d}	$17.3 \pm 0.4^{a,b,c}$	$12.9 \pm 0.6^{c,d}$	$16.2 \pm 1.0^{b,c,d}$	$12.6 \pm 0.6^{c,d}$
($n=3$)	Gel strength (g cm^{-2})	$724 \pm 22^{b,c,d}$	$772 \pm 58^{b,c}$	$634 \pm 41^{c,d}$	$845 \pm 9^{a,b}$	560 ± 54^{d}	994 ± 109^{a}	$905 \pm 42^{a,b}$	982 ± 41^{a}	$813 \pm 40^{a,b,c}$	$767 \pm 102^{b,c}$
2	Carrageenan (%)	8.8 ± 0.4	15.6 ± 0.4	19.8 ± 0.6	11.9 ± 1.3	-	7.5 ± 0.01	-	-	-	-
($n=2$)	Gel strength (g cm^{-2})	951 ± 42	1106 ± 87	935 ± 56	888 ± 107	-	1000 ± 85	-	-	-	-
3	Carrageenan (%)	-	-	20.2 ± 0.5	-	-	-	-	-	-	-
($n=3$)	Gel strength (g cm^{-2})	-	-	967 ± 18	-	-	-	-	-	-	-

Different superscript letters denote differences between the cultivars (Fisher's LSD, $P<0.05$). Note replication in Cycle 2 of $n=2$ ropes due to availability of biomass

culture during the trial. Water temperature ranged from 28.7–31.3ºC (mean 30.1ºC) during the trial (Supplementary Material, Fig. S1). Salinity ranged from 29.2–36.0 ppt (mean 32.4), peaking during late September, then declining (Supplementary Material, Fig. S1). pH ranged from 7.1–8.3 (mean 7.7). Nitrate and phosphate data are summarised in Table S1 (Supplementary material file) but did not show any clear patterns.

Farmer grow-out trials

In the on-farm comparisons, the best-performing cultivar from the common garden trials (i.e. Mamuju) showed superior growth to the three local cultivars at all trial locations (Fig. 3). Morphologically, the Mamuju cultivar (locally called *kotoni Kambunong*) has a long thallus reaching 50 cm, with a larger thallus stem diameter, wider distances between branches with fewer branches compared with the 'local' cultivar (Fig. 4). The 'local' cultivar (*kotoni merah*) grown at the common garden location has a relatively shorter ('medium') thallus length reaching 25–30 cm, a smaller thallus diameter than the Mamuju cultivar ('medium') with shorter distances between branches so that the thallus clumps look denser and more numerous (Fig. 4).

Consistently higher growth was demonstrated by the Mamuju cultivar at all three trial locations (Table 3), with increased biomass of 24% at Wajo (independent t-test, $P_{Adj.} = 0.001$), 217% at Jeneponto ($P_{Adj.} < 0.001$) and 416% at Barru ($P_{Adj.} < 0.001$) locations compared with the local cultivar that the farmers were using prior to the introduction of the Mamuju cultivar (Fig. 3). Production of the Mamuju cultivar was, on average, 824 g m^{-1} for the 45-day

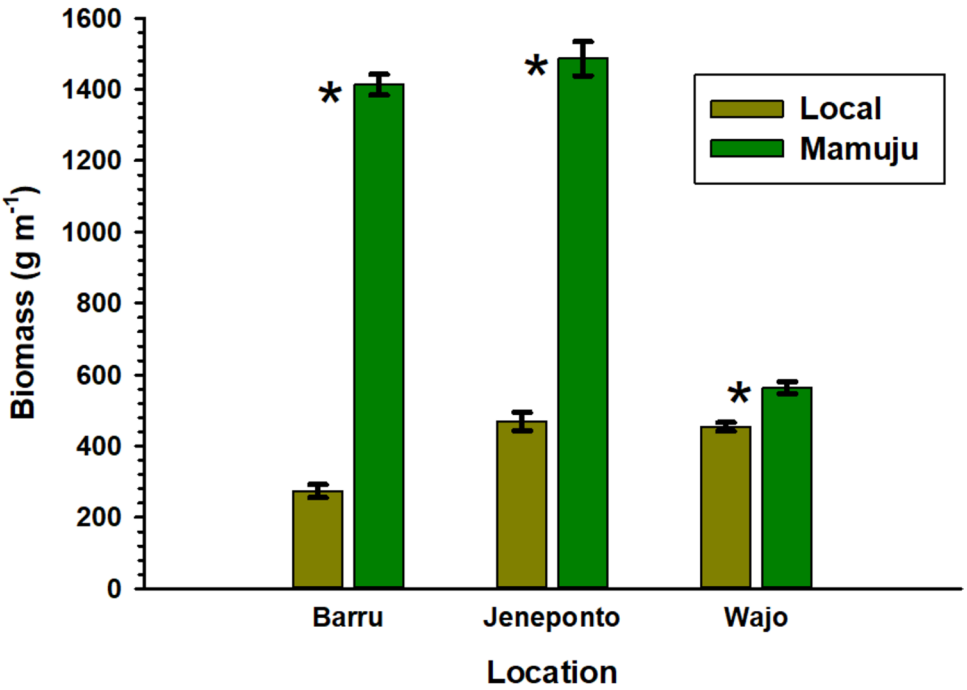


Fig. 3 Mean ± SE ($n = 6$) biomass of local and Mamuju cultivars of *K. alvarezii* harvested after a 45-day farmer grow-out trial at three separate locations (see Fig. 2). * indicates significant difference between the Mamuju and local cultivar at each location (independent sample t-tests, $P_{Adj.} < 0.05$).

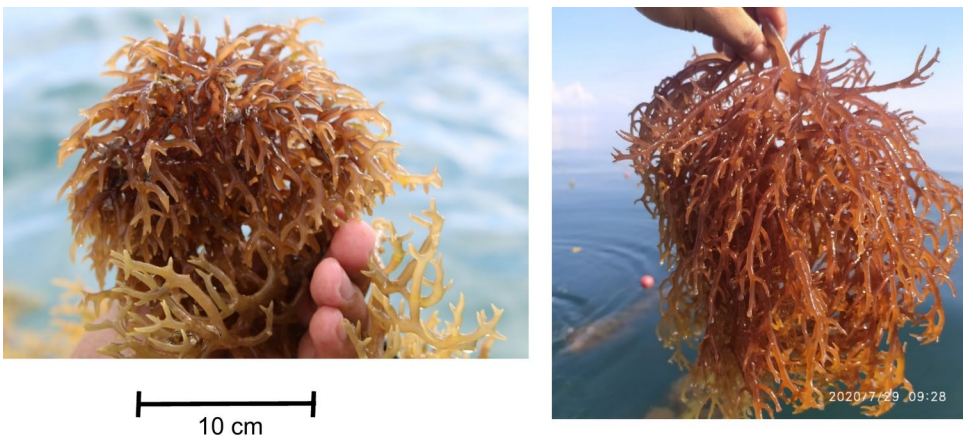


Fig. 4 Representative examples of (left) the 'local' (local name: *kotoni merah*) and (right) Mamuju *K. alvarezii* cultivars (*kotoni Kambunong*) used in the farmer grow-out trials at Boddie village, Pankep, South Sulawesi

Table 3 Biomass (mean ± SE, $n = 6$) and carrageenan content ($n = 1$) at harvest for local and Mamuju cultivars of *K. alvarezii* from one 45-day farmer grow-out trial at three separate trial sites (see Fig. 2). Initial density was 330 g m^{-1}

Parameter	Cultivar	Location		
		Barru	Jeneponto	Wajo
Biomass (g m^{-1})	Local	274 ± 18	469 ± 26	454 ± 12
	Mamuju	1413 ± 29	1486 ± 48	564 ± 17
Carrageenan content (%)	Local	25.7	21.0	31.7
	Mamuju	24.2	24.8	32.3

cycle, equivalent to 6.69 kg m^{-1} y^{-1}, compared to the average of the local cultivars at 0.56 kg m^{-1} y^{-1}. Overall, there was a 1.7- to 4.5-fold increase in biomass across the three farmer trials (final minus initial weights over 45 days), which equates to SGRs of 1.2–3.3% day^{-1} (calculated from Table 3). Although carrageenan content data are only indicative (not replicated), we note that the two highest values were from Wajo and that there were no major differences between the cultivars at Wajo and Barru sites (Table 3). The carrageenan contents of the Mamuju cultivar from the three on-farm trials (24.2–32.3%) were all higher than for the three common garden cycles at Pangkep (19.2–20.2%; Table 2).

Farmer interviews

The farmers interviewed reported general satisfaction with the Mamuju cultivar, and 17 (of 30 farmers interviewed) were still farming this cultivar in 2024 (four to seven years after it was provided). The majority of farmers who had stopped cultivation were from Pangkep District, where all of the surveyed farmers reported losing cultures in 2022 due to extreme weather and ensuing flooding. All cultures of the Mamuju cultivar in the Pangkep area were lost in 2022, and the farmers did not have funds to purchase seedstock (i.e. starter cultures) of Mamuju cultivar; hence, they re-established their cultures using seedstock sourced from nearby locations. It is however noted that some of the *kotoni* (local name for *K. alvarezii,* with roots from its earlier taxonomic classification as *Eucheuma cottonii*) currently produced is possibly still surviving Mamuju cultivar. Farmers in all three locations reported also growing *sacol* strain (potentially *K. striatus* or another morphotype of *K. alvarezii*), and in Pangkep and Barru were growing 'spinosum' (*Eucheuma denticulatum*) as well.

Satisfaction with the performance of the Mamuju cultivar by farmers was very high. Although it received the same farm-gate price as other seaweeds, it was perceived as growing better, being more disease-resistant, and producing well in all seasons, in contrast to previously cultured cultivars. When asked about the perceptions of others involved in the seaweed value chain, the majority of farmers reported that buyers commented on the superior morphology of the Mamuju cultivar, with larger and longer thalli with more branches, and less biofouling. For dried seaweed, they reported good colour and better resistance to breaking compared with other cultivars they had farmed.

Farmers who cultured the Mamuju cultivar recommended this cultivar to other farmers in their vicinity, and 28 farmers (out of 30) reported they know someone who had started growing the Mamuju cultivar (as secondary users through transfer), and that they were aware of yet more farmers interested in starting to grow this cultivar. Reasons for this were reported as the perceived benefits from better growth, improved morphology (appearance of the thallus), better resistance to breaking, and greater total weight (when dried) compared to other cultivars.

Discussion

This study represents the first comprehensive comparison of growth and product quality parameters using 10 different cultivars of *K. alvarezii* sourced from throughout Indonesia. Using a 'common garden' experimental design, where the cultivars were evaluated under the same environmental conditions using standardised culture methods, we demonstrate substantial inter-cultivar differences in both production and product quality, including differences in selected cultivars across three back-to-back 45-day culture cycles. Furthermore, the study reveals that use of a better-performing cultivar of *K. alvarezii* provides increased productivity for commercial seaweed farms, and that the farmers value such research outcomes.

All the *K. alvarezii* cultivars used in these trials were genetically identical with the COI marker (Ratnawati et al. 2020) and the same mitochondrial haplotype (3) as has been identified in all cultured populations of *K. alvarezii* (Zuccarello et al. 2006). It is well established that there is substantial seasonal and regional variation in production and product quality of farmed *K. alvarezii* (Neish 2013; van Oort et al. 2025). This variation can be ascribed to three main influences: genetic variation amongst *K. alvarezii* 'strains' or cultivars (Zuccarello et al. 2006; Lim et al. 2014), different environmental conditions, particularly temperature and nutrient levels (Muñoz et al. 2004; Kotiya et al. 2011), and culture methods, including planting density, depth and culture duration to harvest (Hurtado et al. 2008; Gacura et al. 2026). The 'common garden' approach used in this study removes the second and third of these influences by using a standardised culture method at a single location, leaving genetic variability as the main source of variability in these comparisons (Rose

and Garland 2009; de Villemereuil et al. 2016; Sudatti et al. 2021). Our results show that this genetic variability between cultivars of *K. alvarezii* in Indonesia is substantial and can be used to identify and distribute better-performing cultivars for farming. A similar evaluation by Gacura et al. (2026) in the Philippines demonstrated phenotypic plasticity among four different *K. alvarezii* strains in terms of their growth performance, morphology, biochemistry and susceptibility to ice-ice disease syndrome.

In the first common garden cycle, the cultivars exhibiting the best growth (Manado, Gorontalo, Mamuju and Lombok) yielded from 146–213 g m^{-1}, compared with the poorest performing cultivars (Bantaeng, Lampung and Kupang) which yielded only 23–47 g m^{-1} (Table 1). This difference represents a 3- to sixfold higher production by the best-forming cultivars. The Mamuju cultivar demonstrated consistently high survival (79–88%) across all three cycles and was consistently amongst the cultivars with the highest carrageenan content (Table 2). Across all three cycles the Mamuju cultivar had, on average, the equivalent of 0.76 kg m^{-1} y^{-1} of new growth. Compared with other studies on production of cultured *K. alvarezii*, growth performance in these trials was relatively low (< 1 kg m^{-1} y^{-1} equivalent), noting that the intent of the common garden experiment was to compare performance (growth and survival) across many cultivars, and that the three trial cycles crossed into the 'low' season (September – November) when farmers in Pangkep report that *Kappaphycus* growth is poor, and many switch to the more robust *E. denticulatum*. The productivity of seaweed farms in Indonesia and Philippines is typically low at 1.1–1.4 kg m^{-1} y^{-1}, reportedly because of ice-ice disease (Valderrama et al. 2015). There is also variance across production regions in *K. alvarezii* productivity in Indonesia, with values in Sulawesi ranging from 0.4–1 kg m^{-1} in Gorontalo (Fadilah et al. 2016), 1.2 kg m^{-1} in Buton (Southeast Sulawesi) (Afandi et al. 2015) and up to 2 kg m^{-1} in Bau Bau (Southeast Sulawesi) (Kasim and Mustafa 2017).

Although cultivated *K. alvarezii* have the same mitochondrial haplotype (3) there is substantial phenotypic plasticity amongst 'strains' (Zuccarello et al. 2006; Dumilag et al. 2016, 2023; Simatupang et al. 2021; Gacura et al. 2026), and this was again demonstrated in this study (Fig. 1). However, we did observe some degree of convergence of morphology and colour of the cultivars trialled at the common garden site (Fig. 1). While it is possible that phenotypic plasticity is triggered by non-measured genetic differences, this is unlikely since the plants are clonally propagated. An alternative mechanism for the demonstrated phenotypic plasticity in *K. alvarezii* is that these are triggered by epigenetic interactions or other non-genetic mechanisms. The observed trend of converging morphology and colour when different cultivars are cultivated in common conditions supports this hypothesis that epigenetic factors are influencing *K. alvarezii* cultivar morphology and colour. Additional research on this aspect would be valuable in potentially identifying epigenetic factors affecting *K. alvarezii* cultures.

The differences in performance recorded in the common garden trial were reflected in the performance of the selected Mamuju cultivar when it was compared with 'local' commercially cultivated seaweed (the origins of which are now obscure) at three farming sites in South Sulawesi. The selected Mamuju cultivar demonstrated > 200% higher biomass at Jeneponto and > 400% at Barru locations compared with the local cultivars that the farmers were using at these locations (Fig. 3). In contrast, the Mamuju cultivar demonstrated only 24% higher biomass when trialled against the local cultivar at Wajo (Fig. 3). Still, on average, the Mamuju cultivar had an annual equivalent of 6.69 kg m^{-1} y^{-1} which was more than 10-times the average of the three local cultivars at 0.56 kg m^{-1} y^{-1}. These results indicate that *K. alvarezii* cultivars selected using the common garden approach can dramatically improve farm productivity, but that the level of this improvement can differ substantially between locations.

Seaweed farmers who were provided with the Mamuju cultivar provided very positive feedback on its performance and marketability. With the exception of the seaweed farmers in Pangkep, who had lost their cultures due to extreme weather and associated flooding, the seaweed farmers that we interviewed were continuing to cultivate the Mamuju cultivar five years after it had been introduced. More recently (pers. comm), some farmers have renewed their seaweed cultures using *K. alvarezii* cultures purchased from farms in Mamuju, including Pangkep farmers under direction and support from the South Sulawesi government. The restocking of farms is an important consideration, as seaweed growing seasons are different for all locations, and there are different strategies for dealing with the low season. For example, farmers may switch to culturing *Eucheuma* during periods with higher temperatures and increased incidence of ice-ice disease in *Kappaphycus* (van Oort et al. 2025), accepting the lower price brought by *Eucheuma* compared with *Kappaphycus*.

The need for improved cultivars of seaweed is recognised as a critical gap, limiting the continued development of Indonesia's seaweed farming industry (Permani et al. 2024). We conclude that the common garden approach is valuable in comparing the performance of seaweed cultivars to identify those with superior performance characteristics (growth and quality) for provision to commercial seaweed farms. Identifying, then sourcing, from key areas offers an immediate restocking alternative to seed purchases from neighbouring farmer areas, complementing regional research efforts on tissue-culture and domestication of wild-type eucheumatoids to address perceived

issues in genetic diversity (Faisan et al. 2024; Gonzaga et al. 2025). Despite some cultivars demonstrating superior performance, the level of this performance varies between locations and across seasons, suggesting that common garden evaluations may be necessary at regional scales to maximise the benefit of this approach for commercial seaweed farming, with year-round assessment to evaluate disease and environmental relationships. Congruent with this approach, an effective distribution system for selected high-performance cultivars is necessary. Indonesia has a limited system of seed nurseries (*kebun bibit*) associated with the Technical Implementation Units (TIUs) of the Ministry of Marine Affairs and Fisheries (Ruhon et al. 2024), and this network could provide a starting point for development of regional common garden experimental sites, which could also act as distribution centres for commercial farms. However, given the limited number of TIUs, additional distribution mechanisms would be necessary to develop and distributed selected *K. alvarezii* cultivars to seaweed farming sites across Indonesia. More broadly, the common garden approach is a technologically simple system that lends itself to application in other seaweed farming regions to improve farm production and support livelihoods in coastal communities.

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Data availability The data that has been used is confidential, subject to the intellectual property policies of BRIN (National Research and Innovation Agency, Indonesia).

Declarations

Ethics approval University of the Sunshine Coast Human Ethics Committee Approval Number A/17/997.

Competing interests The authors declare no competing interests.

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