



Assessment of genetic and phenotypic diversity of the giant kelp, *Macrocystis pyrifera*, to support breeding programs

Carolina Camus^a, Sylvain Faugeron^{b,c}, Alejandro H. Buschmann^{a,*}

^a Centro i-mar, CeBiB, Universidad de Los Lagos, Puerto Montt, Chile

^b Centro de Conservación Marina, CeBiB, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile

^c UMI 3614 Evolutionary Biology and Ecology of Algae, CNRS, Sorbonne Universités UPMC Univ. Paris 06, Pontificia Universidad Católica de Chile, Universidad Austral de Chile, Chile

ARTICLE INFO

Keywords:

Breeding
Genetic diversity
Phenotypic diversity
Microsatellites

ABSTRACT

The accelerated development of seaweed aquaculture is stimulating research on the genetic drivers of phenotypic diversity of the target species, in order to optimize breeding strategies, to help determine the choice of source populations, and for the selection of traits and varieties that fit with the environmental variability of the production site. This study investigates the spatial variation of the genetic and phenotypic diversities in natural populations of the giant kelp *Macrocystis pyrifera*, and evaluates the potential for modifying agronomic traits through controlled breeding. Nine microsatellites and 12 morphological traits were used to describe the distribution of diversity present along the Southeastern Pacific (SEP) Coast. We expected concordant patterns of spatial discontinuities if the genetic background was driving morphological divergence across habitats. Crossing experiments were made to assess the heritability of specific traits and evaluate the performance of the F1 generation in the laboratory and in open sea cultivation respectively. Our results revealed four genetic clusters along the latitudinal distribution of *M. pyrifera* populations, tightly correlated with the existence of major environmental discontinuities. These clusters also matched clusters of morphological diversity, suggesting that both morphological and genetic diversities responded to the same environmental drivers. In crossing experiments, no significant differences were detected between selfed and outbred F1, in morphology, growth and chemical components, but a high variability among all different crosses was observed, revealing a high degree of heritable phenotypic variance. Although, the results suggest that the morphological variation of *Macrocystis* along the SEP coast is strongly driven by the genetic background. Our controlled crosses were also indicative of a high potential for using this genetic variability in breeding programs for sustainable aquaculture development.

1. Introduction

The use of seaweeds for food/feed, pharmaceuticals, textiles, cosmetics, and biofuels [1–5] and the continuously growing demand for raw material, is rapidly changing the way that we humans interact with this natural resource [6]. Encouraged by this increasing demand and the need to reduce the over-exploitation of natural resources, seaweed farming is expanding across several continents from East Asia to Europe, South America and East Africa [7]. Within aquaculture, the global production of seaweeds is 27.3 million tons (27%), and it has increased by 8% per year over the past decade [8].

Under this scenario, seaweed farming requires the urgent development of breeding programs to increase yield and optimize other relevant agronomic traits [9,10]. There is a large amount of information on the development of macroalgal strains in red and brown algae

[11,12,13]. However, the genetic science behind seaweed breeding and domestication is still in an initial phase, with little conceptual and empirical progress [14]. Several challenges related to the biological peculiarities of algae and their environment are yet to be faced. For instance, the marine environment is more complicated to manipulate than terrestrial environments, where water and nutrient supply, ploughing and other manipulations modify the physico-chemical properties of the soil, and avoid competitors, predators and most pests and pathogens. Such manipulations are generally not possible in the sea, without significant logistical and infrastructure costs, which are sometimes accompanied by unwanted side effects [15]. Therefore, the increase in productivity must strongly rely on the modification of heritable traits. Yet, the genetic improvement of any agronomic trait must ensure the retention of adequate genetic variance in the targeted traits in order to ensure sufficient scope for adaptation to local

* Corresponding author.

E-mail address: abuschma@ulagos.cl (A.H. Buschmann).

environmental variation. Another major difference with land plants, where current breeding efforts are concentrated in already domesticated strains, is the use of wild variants for most seaweed aquaculture initiatives [16,17]. Some of the cultivated algal species have never gone through a selective breeding process, based on genetic knowledge. Currently, no more than eight species are in the early stages of domestication [18]. One possible reason for this maybe the ease with which selected strains from wild populations can be cloned in order to establish a new seaweed farm. On the other hand, the complex life histories of algae, add additional conceptual and practical constraints to the implementation of breeding programs [18]. Indeed, trait correlations among life cycle stages may have negative consequences on overall production and/or breeding efforts [19]. For example, selecting for growth rate in the farmed red alga *Gracilaria chilensis* caused the dominance of heterozygous diploids that lost their capacity for sexual reproduction [20,21,22] and contributed to the critical loss of genetic diversity observed in this species [20]. Strong genetic diversity losses in cultivated populations can have serious consequences for the adaptability of these species and their susceptibility to pests and diseases [6,23,24,25,26,27].

One of the main challenges that seaweed-breeding science is currently facing is the lack of general knowledge on the drivers of phenotypic diversity. While a large body of literature has analyzed phenotype responses to environmental variation, relatively little is known about genetic determinism of algal traits and their interactions with environmental determinants. Quantitative genetics approaches on algal models, such as QTL analysis [28,29], have recently emerged, and should provide valuable tools to assist breeding strategies in the near future. However, because most cultivated seaweeds are not yet domesticated, the production of new varieties must rely on an initial genetic pool collected from natural populations. Therefore, a critical initial stage in the establishment of a breeding program is the acquisition of solid knowledge concerning the natural variation in both the phenotypic and genotypic diversities [6]. Several fundamental questions can be tackled from such knowledge: 1) can selection (either natural or artificial) modify traits of interest such as growth rate or shape (among many other traits)? By investigating signatures of evolutionary divergence between environments within the species range, it is possible to infer the evolvability of the species of interest under natural conditions, which is related to the capacity of different traits to accumulate additive genetic variation. The existence of such genetic diversity is essential to the success of trait improvement by selective breeding. 2) Can new varieties be cultivated anywhere or should landraces be established? Because aquaculture systems are deeply influenced by the natural environment, which cannot be easily modified or controlled, it is likely that selected strains or wild progenitors that evolved local adaptations will not be able to grow optimally in non-native environments. In this context, breeding strategies based on selection of local variants should maintain the genetic diversity necessary for optimal growth in the farm environment to secure the sustainability of the production. 3) Should breeding strategy be oriented towards hybrid vigor or “pure” (i.e. inbred) lines? The presence of inbreeding in natural populations may promote inbreeding depression. In this case, hybrid vigor is expected when crossing different inbred lines. However, if local adaptation has taken place in natural populations, hybrids might break down optimal allelic combinations for specific environments. Also, depending on the level of local genetic diversity, and how representative of this diversity the collection of the initial progenitors was, a breeding program could suffer from high rates of inbreeding and loss of allelic variation if the relationships between the breeding candidates were not considered when making selection decisions. Therefore, efforts to develop diversified germplasms for experimental evaluation of inbreeding effects and local adaptation may complement studies of natural populations, as well as promoting backup conservation strategies [30].

This study aims to investigate the spatial structure of the genetic and phenotypic diversities of the giant kelp, *Macrocystis pyrifera* (L.) C.

Agardh. This species is under a strong and increasing exploitation pressure, mainly for alginate production and as a source of feed for abalone [31]. Regulatory restrictions on kelp exploitation in many countries and the increasing demand for kelp biomass challenges the sustainable exploitation of natural populations, from which the large majority of the biomass is obtained. Biomass production through cultivation is an alternative that is being explored in several countries across its wide distribution range. In Chile, new legislation allows incentives for cultivation and repopulation of seaweeds, providing a positive environment for the installation of a kelp farming industry in the country. Pilot-production has demonstrated that 124 wet ton·ha⁻¹ of *M. pyrifera* can be achieved using wild individuals to seed ropes for suspended systems [32]. The development of *M. pyrifera* aquafarming is expected to emerge rapidly for several reasons: established procedures for cultivation in hatcheries [33] and open ocean [32] allow for the testing of the agronomic performance of a large array of genotypes and pilot scale production; technology used to convert biomass to bioethanol implemented at the pilot scale [34,35]; and identification of novel components for food and pharmaceutical uses that add value to the biomass production [5,36,37].

M. pyrifera is considered to be a highly plastic species [38,39], yet some morphological traits were considered to express a strong phylogenetic signal. Indeed, the spatial distribution of different morphotypes based on blade and holdfast shape along the coast was highly correlated with the presence of divergent clades of an ITS2-based phylogeny [40]. Using mitochondrial DNA, Macaya and Zuccarello [41] reported low genetic diversity across the SEP coast but a concordance with the two major biogeographic discontinuities at 33°S, and 42°S, suggesting that environmental heterogeneity may be contributing to the distribution of the genetic diversity. Besides the relevance of this information, limited resolution of the molecular markers and the morphological survey restricts our understanding of the spatial patterns of phenotypic variation. The reduced genetic diversity and divergence among habitats or distant regions, and the high phenotypic plasticity were considered as strong arguments for a recent evolutionary history in the southern hemisphere where little or no adaptive divergence has occurred. Consequently, if natural selection had little or no impact on the species phenotypic diversity, it was considered that breeding and strain selection would be insufficient to modify traits and improve productivity under farming conditions. In this study, we challenged this view by developing a comparative study of genetic and morphological divergence across parts of the South American distribution range, with special emphasis on the region of Chiloé where environmental discontinuities are well known.

We quantified the genetic diversity and its spatial distribution in *M. pyrifera* across the SEP coast, and its association with morphological diversity. Secondly, we investigated the potential for modifying traits through controlled breeding by testing morphological, growth and chemical differentiation among crosses of *M. pyrifera* with different genetic backgrounds but cultivated in a common garden. Results are discussed in the context of seaweed domestication and sustainable production.

2. Materials and methods

2.1. Morphological analyses

Adult sporophytes were collected at 16 locations along the Chilean coast (Table A1). At each site, between 20 and 30 mature individuals were collected along a transect of approximately 600 m by scuba diving, and transported immediately to the laboratory in boxes cooled with ice packs. Morphological analysis involved measuring the following characters of each thallus: number of stipes, total thallus length, total wet weight, number of blades, holdfast diameter and height. In addition, the following characters were measured for ten randomly selected blades per thallus: maximum blade length and width, blade angle with the stipe,

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