Letter

Seaweed cultivation: potential and challenges of crop domestication at an unprecedented pace

Introduction

The world-wide macroalgae industry has increased exponentially over the last 50 years (Fig. 1a,b). Between 2003 and 2012, its average annual growth was 8.13% in quantity and 6.84% in monetary value (Food & Agriculture Organization of the United Nations (FAO), 2014). Over 23 million tons of macroalgae (dry weight) were produced in 2012 from aquaculture, which were worth over six billion US$ (FAO, 2014). Approximately 83% of this biomass is produced for human consumption while the remainder is used as fertilizers, animal feed additives and, increasingly, for medical and biotechnological applications (McHugh, 2003). Seaweeds have a recognized, though barely tapped, potential for biotechnology and sustainable biofuel production (Mazarrasa *et al.*, 2014). A more immediate expansion driver is, however, the prospect that seaweed farming can improve the sustainability of fish and shellfish aquaculture in integrated cultivation initiatives. With an annual growth of nearly 10%, fish farming is the world's most rapidly expanding food-producing sector and represents a major stake toward meeting soaring global demand for dietary proteins over the forthcoming decades (Duarte *et al.*, 2009). Encouraged by these demands and efforts to reduce the over-exploitation of natural resources, seaweed farming has been expanding rapidly across several continents from south-eastern Asia down to South America and East Africa (Rebours *et al.*, 2014).

A recent seaweed domestication history

Though algae have been traditionally cultivated in Asia for centuries (Dillehay *et al.*, 2008; Buchholz *et al.*, 2012), selective breeding of macroalgae is a much more recent endeavour. China, in particular, has developed seaweed breeding programmes since the 1950s. For example, > 20 commercial varieties of the kelp *Saccharina japonica* have been developed, with improved yield, quality, disease resistance or stress tolerance (Zhang *et al.*, 2007). However, the rapid expansion of the algal industry and a tendency to see it as a large 'global crop' (that shares identical or very similar seedling genetic background across many locations) is leading to the emergence of multiple inter-related concerns. First, seed quality is a major issue throughout the industry, mainly due to the widespread clonal propagation techniques (e.g. the carrageenophytes *Eucheuma* sp. and *Kappaphycus* sp.) or propagation via sexual reproduction from a limited pool of parent individuals (e.g. kelps, such as *Undaria* sp. or *Saccharina* sp.). The resulting phenotypic instability repeatedly leads to discard cultivars from the production lines shortly after their introduction (Shan *et al.*, 2011). As detailed in Robinson *et al.* (2013), improving our understanding of the genetic resources and natural variation available in wild stocks (e.g. Voisin *et al.*, 2005; Liu *et al.*, 2012) is key to building more efficient, science-based breeding programmes, improve seed production systems and curb inbreeding.

Gene swamping, introduction of non-native genotypes and invasiveness

Throughout history, the commercial introduction of non-native organisms has contributed to the involuntary spread of alien species such as *Undaria pinnatifida* (wakame, Grizel & Heral, 1991; Voisin *et al.*, 2005). In fact, many introduced macroalgae have become naturalized within a matter of years and, in some instances, raise concern with regard to their spread, such as *Gracilaria salicornia* and *Kappaphycus alvarezii* in India, Hawaii and East Africa (Conklin & Smith, 2005; Nelson *et al.*, 2009; Halling *et al.*, 2013).

Non-native species incur huge environmental and economic damage (Pimentel *et al.*, 2001). World-wide, marine ecosystems are already those most affected by biological invasions despite the existence of regulations that restrict the release of organisms in the open sea (e.g. Regulation no. 708/2007; no. 535/2008 and Regulation (EC) no. 506/2008 amending Annex IV to Council Regulation (EC) no. 708/2007). Containment and restoration measures are particularly difficult to deploy *a posteriori* in the marine environment and their cost was recently estimated at £40 million per year for the UK industries alone (Williams *et al.*, 2010).

Thus, existing and draft policies typically forbid or severely restrict the use of non-native genotypes in seaweed aquaculture. However, while slowing down the industry's growth, such restrictions are fundamentally inadequate to counter the risk of 'crop-to-wild' gene flow: even when native genotypes are cultivated, their capacity to cross-hybridize with native stocks may result in the introgression of crop genetic material into wild populations. Such gene swamping is now extensively documented in land agriculture and animal aquaculture (Manchester & Bullock, 2000; Jiang *et al.*, 2012; Ellstrand *et al.*, 2013) and is known to have profound consequences on the genetic structuring and evolution of wild populations. Ultimately, it also leads to an impoverishment of the genetic resources usable for selection and introgression of desirable traits into cultivated breeds. A factor potentially aggravating this issue is that the phenotypic traits typically sought after by

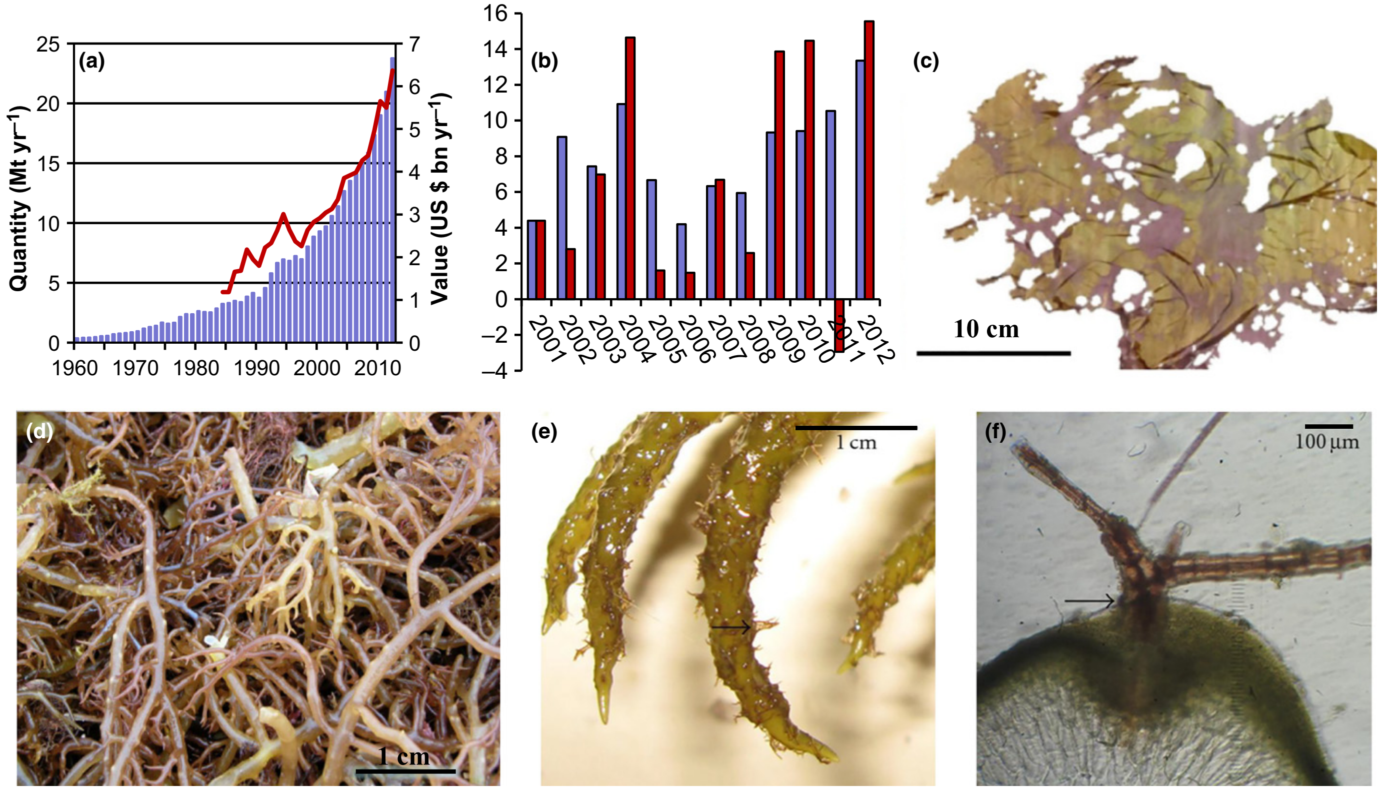

Fig. 1 Diseases, pests and abiotic stressors are major challenges to the global macroalgae aquaculture. (a) Production of macroalgae biomass through aquaculture (Mt, histograms) and value (billion US$, red curve) over the period 1960–2012 (FAO, 2014). (b) Corresponding annual growth rate in (%) of the global aquaculture production in volume (blue bars) and value (red bars). (c) 'Chytrid blight' caused by the oomycete *Olpidiopsis porphyrae* on laver (*Pyropia* sp.), an edible seaweed used as sushi wrap (reproduced, with permission, from Klochkova *et al.*, 2012). (d) Thallus bleaching ('ice–ice' symptoms) caused by a variety of stressors on the carageenophyte *Kappaphycus alvarezii*. (e, f). Goose-bumps (*Neosiphonia apiculata* infestation, arrows) on *K. alvarezii* (reproduced from Pang *et al.*, 2011).

breeders, in particular, easy reproduction and fast growth, might favour the spread of cultivated genotypes.

Crop to wild gene flow is efficiently mitigated both in animal aquaculture and land-based agriculture by the sterilization of farmed individuals. For example, sterilization of cultivated Atlantic salmon has been recommended on these grounds as far back as 1991 (ICES, 1991). Unfortunately, the gene flow from seaweed breeds to wild stocks remains practically unmeasured, an essential step to inform future conservation initiatives. Although not yet widely available, sterilization technologies for seaweeds are scientifically within reach and should be considered to mitigate gene swamping and invasiveness. An additional benefit of developing sterile algal strains might be to offer a route towards the protection of the breeder's intellectual rights.

Multifaceted disease and pest management concerns

The current over-reliance of the industry on genetically uniform genotypes increases the vulnerability of the cultivated species to abiotic stressors, pests and pathogens. The severity of laver red rot and 'chytrid' diseases, caused by oomycete pathogens *Olpidiopsis porphyrae* and *Pythium porphyrae* has been increasing as a result of farming intensification (Ding & Ma, 2005; Gachon *et al.*, 2010; Fig. 1c). Recently, a dramatic decline in production has also been seen in many carragenophytes (*Kappaphycus)* farming countries (e.g. the Philippines and Zanzibar). Such production deficits are mainly attributed to rising sea temperatures, which causes bleaching of the thallus, making the cultivated individuals more susceptible to viruses and bacteria from the genera *Vibrio*, *Cytophaga*, *Pseudomonas*, *Pseudoalteromonas*, *Halomonas* and *Flavobacterium*, as well as to diseases and epiphyte infestations, such as 'goose-bumps' caused by filamentous red algae of the genus *Neosiphonia* spp. (Vairappan *et al.*, 2008; Hurtado *et al.*, 2013; Fig. 1d–f).

The protocols that are currently used to mitigate crop losses are rudimentary and often too costly for small farmers and cooperatives. Most involve the complete removal of seedlings, which requires the start of a new production cycle. This method is used in the Philippines and Malaysia, mainly to remove epiphytes from the carrageenophytes (*Kappaphycus alvarezii* and *Eucheuma denticulatum*). Chemical treatments can also be used, but are known to cause side effects on the final desired product (e.g. acid treatment on laver; Klochkova *et al.*, 2012; Park & Kim, 2013).

Moreover, in contrast to land-based agriculture, the nature and epidemiology of seaweed pathogens is dramatically understudied. Causative pathogens can sometimes be difficult to identify, partly because many remain uncultivable by current microbiological methods (Gachon *et al.*, 2010). Previously unknown species or even groups are typically discovered when a new culture is being introduced, as shown by the recent description of the azoosporic chytrid pathogen *Paraphysoderma sedebokerense* (James *et al.*, 2011).

A third insidious long-term issue is the impact of pests on native stocks. Most are caused by the inadvertent introduction of non-native pathogens. In animal aquaculture, this is exemplified by the plague pathogen *Aphanomyces astaci* imported from America which now threatens native European crayfish with extinction (Longshaw, 2011). Farmed species can also act as a reservoir of parasites (e.g. sea lice infecting farmed salmons causing a decline of native fish stocks, Hutchings *et al.*, 2012).

Conclusions

Macroalgae cultivation holds great economic potential as well as the potential to increase the sustainability of fish farming practices through integrated systems. It also offers development and social alternatives in underprivileged coastal communities throughout the world, where over-fishing is often ripe. However, history has repeatedly shown that intensive farming and domestication are accompanied by profound and often irreversible consequences on biodiversity. To guarantee the sustainability of algal cultivation, and its social acceptability as an environmentally sustainable activity, a coordinated effort in fundamental research is urgently required to assess genetic resources and develop adequate genetic conservation policies, that are, to date, nearly nonexistent. It is also important to start investigating the long-term environmental footprints of algal cultivation beyond immediate localized impacts such as decreased light, shifts in seawater temperature and nutrient availability. This is particularly true for seaweed cultivation in coastal ecosystems since *a posteriori* containment and disease management measures are both far more challenging and costly to implement, and far less efficient than the implementation of good practices regulated by science-based preventive policies.

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