

# Chapter 5

## Ecology



**Detlef Bartsch and Enrico Biancardi**

**Abstract** The traits of *Beta maritima* have been reviewed and summarized from a number of recent and classical publications dealing with the ecology, morphology, and whole plant physiology of the species. Because few papers have been written only on *Beta maritima*, most information comes from cultivated forms of *Beta vulgaris*. A striking feature of *Beta maritima* gleaned from this review is how variable and adaptive it is. The species is fairly plastic allowing it to live in many different environments. This capacity for adaptation to the local environmental conditions has been correlated with breeding system and with the rapid change in reproduction systems. This is evident in the differences between the Mediterranean populations (easy bolting, short life cycle, sprangled taproot) and those growing the sea coasts of northwest Europe or other parts of the world. This chapter provides the reader with a comprehensive overview of the plant and populations to answer the question: What is *Beta maritima*?

**Keywords** *Beta maritima* · Habitat · Survival · Seed dispersal · Floating seed · Gene flow

### 5.1 Survival Strategies

The current climate changes require adequate fitness in the surviving individuals, species, and genotypes (Wagmann et al. 2010). In other words, to improve its chance of survival, every wild population can optimize the fitness to environment by modifying its timing of germination, reproduction time, life span, etc. (Hautekèete et al. 2009; van Dijk 2009b). These strategies in reproduction are crucial when rapid adaptations are required (van Dijk 2009a), particularly in the current situation of climate

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D. Bartsch (✉)  
Federal Office for Consumer Protection and Food Safety, Mauerstrasse 39-41, 10117 Berlin,  
Germany  
e-mail: [detlef.bartsch@bvl.bund.de](mailto:detlef.bartsch@bvl.bund.de)

E. Biancardi  
Formerly Stazione Sperimentale di Bieticoltura, Rovigo, Italy

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change toward higher temperature and reduced rainfall, at least in Europe (Jones et al. 2003; Jaggard et al. 2010). If temperatures rise, it may require variation in the day length needed for flowering induction in biennial sea beet (van Dijk and Hautekèete 2007). From this perspective, sea beet could reduce rapidly such as its day length requirement for entering in advance the reproductive phase. This involvement of population genetics (Crow and Kimura 1970; Hartl and Clark 1997) will be briefly summarized.

Seed dormancy plays a significant role in the survival of individuals within wild populations. Germination in nondormant seed depends only on current conditions. On the other hand, dormant seed undergoes a long-lasting exchange of information with the environment to remove the inhibition factors which hinder germination. Seeds subjected to drought and cold periods delay time and rate of germination, demonstrating the existence of inhibiting mechanisms (Wagmann et al. 2010). In field and greenhouse experiments, about 40% of the total sea beets seedlings germinated and developed from dormant seeds. The dormancy trait seems maternally inherited, is highly variable and have a narrow-sense heritability of  $h^2 = 0.40$ , which may indicate a sufficient ability of sea beet populations to react in the presence of rapid environmental changes (Wagmann et al. 2010).

Some of these traits play an important role in survival of sea beet populations. For example, the relatively large shape of the seed ball and embryos observed in Afghanistan and Iran could improve the seedling's chances of survival during the critical first stages of pre-germination and germination in difficult environments (Krasochkin 1959). According to Hautekèete et al. (2009), the factors influencing the life history strategies are (i) mortality; (ii) availability of resources; (iii) age at maturity; and (iv) climate.

(i) Mortality due to abiotic stresses and diseases plays a central role in population fitness. The dynamics in 21 Adriatic Sea beet populations were studied by Bartsch and Schmidt (1997). They demonstrated that, under favorable conditions, some populations doubled the number of plants present the year before. In this case, it means that only one out of about 10,000 seeds produced by each plant developed an average of one plant surviving the first year. Under such extremely severe selection pressure and in the presence of long-lasting diseases, it is believed that individuals endowed with some degree of genetic resistance or tolerance should be favored in reproduction and survival in presence of that specific disease. In other words, sea beet undergoes, year after year, a sort of natural selection in situ against adverse agents. The fittest plant reproduces faster than the rest of population and rapidly replace the susceptible individuals. This seems not always to be true. It is well known that the Danish sea beet accessions WB41 and WB42 displayed good rhizomania resistance even though they were sampled in fully BNYVV free locations (de Biaggi et al. 2003; Gidner et al. 2005). In soils of Adriatic shores, where sea beet population developed the first source of monogenic rhizomania resistance (Biancardi et al. 2005), Bartsch and Brand (1998) ascertained the absence of BNYVV in the soil. Notwithstanding, some populations have proven very resistant. The foreign origin of wild populations could explain this disagreement.

(ii) Concerning the availability of resources, Hautekèete et al. (2009) stated that the availability of water, nutrients, light, as well as the length of the growing season can influence the photosynthate accumulation and life tactics of *Beta maritima* populations. Increasing resources should hasten the reproduction cycles, whereas the reduced resources could require more time from the plant for flowering and setting seed.

(iii) Age at maturity (age at first reproduction) is also influenced by the available resources. Inadequate resources delay the time until first reproduction and reduce the vegetative growth as well. The seed bearer plant needs adequate time to store enough energy for successful seed yield (Hautekèete et al. 2009).

(iv) Of course, the climate factors—latitude, altitude, distance to the sea, and so on—play a key role in both ages at maturity and survival strategies.

For survival, wild plants such as sea beet must allocate their photosynthate either for reproduction, or for survival, or both. The annual individuals “do not store a large quantity of food in their roots” (De Vries 1905), which remain thin even at the time of flowering. Reproductive effort is higher and invariable for annual or semelparous plants (i.e., they die soon after the very first flowering and setting seed). Normally sea beet is iteroparous, living two or more years, but the behavior can be strictly semelparous in annual plants. The possibility of producing seed once in some period of the year is a successful strategy of reproduction in unpredictable and difficult environments, like the Mediterranean seashores (Hautekèete et al. 2001). On the other hand, the need to survive is more important in an iteroparous plant (living several years and producing seed annually), which is much more influenced by the environment and, above all, by nutrient availability (Hautekèete et al. 2001). Allocation for reproduction and for survival are inversely correlated in iteroparous beets, the opposite happens for the annual and semelparous sea beet. Reproductive effort is inversely correlated also with the life span (Hautekèete et al. 2001).

The genes can be used to increase the local genetic variation (Viard et al. 2004). Transmitting only the male traits, pollen is the prevalent means of dispersal, but seed, which carries both male and female factors, should not be discounted, especially because of the easy movement of sea beet seed by seawater and other means (Ennos 1994). An analysis of the gene dispersal patterns in *Beta maritima* was attempted by Tufto et al. (1998). The dispersal into new localities happens in different ways: (i) unintentional or natural introduction of seeds; (ii) naturalization of cultivated genotypes; and (iii) combinations of the former processes with composite intercrosses via pollen among the *Beta vulgaris* complex (Driessen 2003). The dispersal of sea beet along the marine sites happens mainly through the corky multi-seeded glomerule, obviously adapted to drift dispersal by means of seawater (Dale and Ford-Lloyd 1985; Sauer 1993; Wagmann 2008). The seed, also fitted to spreading by wind (Hautekèete et al. 2002; Smartt 1992), is washed away from the beaches during storms and can float and be transported by the sea currents covering up to 50 km per day (Fievet et al. 2007). The wind also can move the seeds carried into new environments by the seawater out of the splash zone to where they can germinate

and grow. Tjebbes (1933) confirmed that “the seed can float for days without losing germination capacity”. According to Driessen et al. (2001), after 20–25 weeks in salty water, the seed retained 2% of its germination ability. The sea beet populations located on the southern coast of Norway originated probably from the English Islands (Engan 1994). The same was hypothesized by Rasmussen (1933) for few populations located on the Swedish shores. Andersen et al. (2005) evaluated the genetic distance and found that the Danish and Swedish populations are closely related. Both are more similar to the Irish than the French and Italian sea beet populations. The presence of very small and isolated populations in remote, in other ways inaccessible shores of the North Sea, Baltic Sea, and British Islands, is evidence of the dispersal of sea beet via seawater (Dale and Ford-Lloyd 1983; Letschert et al. 1994). This is true also for the Mediterranean and Adriatic populations (Biancardi, unpublished).

## 5.2 Dispersal

The multigermy of sea beet seed is believed to be essential for the species dispersal in new and remote sites (Dale and Ford-Lloyd 1985). In fact, the trait is necessary to overcome the normally high degrees of self-sterility, which could hinder the reproduction of isolated plants in new localities. It is well known that the beets developed from the same seed ball are genetically different because each embryo originated from different pollen grains and most likely from different male parents, thus allowing the cross reproduction in the new site by the first plants, termed founder population, originating from a single seed ball (Dale and Ford-Lloyd 1985). These authors demonstrated the interfertility of beets developed from the same glomerule. The normal level of genetic variability necessary to better fitting the new environment can be guaranteed by pollen coming from the same source of the seed. Obviously, the chances of stable colonization in this way are extremely low since it reduced according to the square of the distance. As written above, of the several thousand seeds produced by a plant, only few plantlets survive around the source. But in nature, the time is almost never a limiting factor (Biancardi, unpublished).

There is also the possibility of seed dispersal by means of animals (Driessen 2003). Indeed, beet seed is attractive to birds, especially if monogerm or bigerm seed. The seed ball easily can be opened with the beak to separate the edible embryo from the woody pericarp. Some seed may be swallowed entire and pass unharmed through the digestive system. In this way, it may be transported for considerable distances. This possibility of dispersal could explain the presence of sea beets in continental areas otherwise inaccessible, such as Mount Etna (Letschert and Frese 1993), or up to 1,800 m altitude in Caucasian Mountains (Aleksidze et al. 2009), or Mount Olympus (Greece) for *Beta nana* (Frese et al. 2009). On the Adriatic coasts, sea beet is spread only in sites always located near the sea, confirming that the seed dispersal happens mainly through the saltwater. In fact, usually, the sea beet can be found only in the last 150–250 meters in the banks of the river estuaries (Biancardi unpublished).

Dahlberg and Brewbaker (1948) hypothesized that the wild beets growing in Santa Clara County, California, USA, were introduced by the Franciscan Fathers between 1779 and 1780, mixed together with beet or other kinds of seed (Fig. 5.1). Another mean of long-distance dispersal of sea beet might have been the sand or soil ballast used some centuries ago in the sailing vessels (Bartsch and Ellstrand 1999). The sand was collected near the harbors, possibly containing sea beets, and put on board for improving the stability of the empty ships. The ballast was discharged once the ship had arrived before loading merchandise. In agreement with this hypothesis, some pure sea beet populations that were identified around the harbor of Santa Barbara, California USA, and analyzed with allozymes (UPGMA), showed a close relationship to Spanish accessions. In fact, ships came frequently at that time from Cartagena, Spain, after sailing the Pacific Ocean and both *Beta maritima* and *Beta macrocarpa* are fairly widespread on the Spanish Atlantic and Mediterranean coasts (Christensen 1996). Driessen et al. (2001) and Poulsen and Dafgård (2005) explained in a similar way the dispersal of sea beet from the British Islands to the Baltic Sea, and from the Danish to the German coasts. The same could have happened for sea beet, currently very widespread in the lagoon of Venice, through long-established ship trade with the eastern Mediterranean harbors. Carsner (1928) speculated that the wild beets present in several Californian localities were either *Beta maritima* or crosses between sea beet and cultivated varieties. Commercial seed containing unwanted  $F_1$  crosses with sea beet pollen is another mean for long-distance dispersal of *Beta maritima* germplasm.

Fénart et al. (2008) and Villain et al. (2009) explained the spread of sea beet into the current locations and into remote sites as a consequence of the last Quaternary glaciations and the subsequent plant recolonization. The introduction of sea beet at Østfold, Norway, a location quite far from the sea seems due to glaciations as well



**Fig. 5.1** Flowering sea beet in salt marsh environment of California (USA)

(Batwik 2000). Villain et al. (2009), based on molecular analysis, speculated that the *Beta maritima* had two different evolutionary lineages: (i) European, carrying the mutation “LF 118”, and (ii) Balkanic–Adriatic, with the mutation “LF 124”. After the last quaternary glaciations, the North Atlantic coasts were colonized by the plants that survived in the North African and Spanish refuges (Villain 2007). Those that survived in the eastern refuges expanded into the Mediterranean basin. In other words, the species coming from their southern refuges, spread toward the European areas, which became free of ice in the late upper Neolithic (Rivera et al. 2006). Villain et al. (2009) hypothesized also that the sea beet colonization of the western Mediterranean basin should have happened more recently than the Eastern region.

Krasochkin (1960) considered the Mediterranean sea beet as the primary form of the populations adapted to grow far from the sea. In agreement with this hypothesis, the distribution patterns of the specific allozyme *Acpl-2* (Letschert 1993) suggested the existence of two distinct gene pools (Atlantic and Mediterranean), with different morphological traits as well. The first form flowers preferably later (if not in the second year), the leaves are more succulent and thick, the seed stalks are more prostrate, and the morphology is much more uniform than the Mediterranean (Letschert and Frese 1993). In the last one, the monogerm seeds are rather rare. The genetic diversity evaluated with the same allozyme is quite similar among the plants of the same population and between neighboring populations (Letschert 1993). This polymorphism seems caused by the variable habitat. Shen et al. (1996) confirmed that “sea beet can broadly be subdivided into northern and southern European forms, the first being biennial and the many of the second being annual”.

### 5.3 Gene Flow

Cases of pollen flow from crop to wild beet have been noted in France (Lavigne et al. 2002; Viard et al. 2002; Arnaud et al. 2003). Pollen produced by the large seed crop area (around 3,000 ha each containing around 10,000 flowering male-fertile beets) located in Emilia-Romagna, Italy, did not seem to have contaminated the sea beet populations along the Adriatic coast ranging from 2 to 90 km (Bartsch and Schmidt 1997; Bartsch et al. 2003). According to Schneider (1942), one hectare of beet seed crop with around 25,000 flowering beets produces approximately 25 trillion pollen grains.

The gene flow in the opposite direction (wild to crop) also seems low (Bartsch and Brand 1998). Andersen et al. (2005) analyzed 18 sea beet populations collected in different localities and confirmed that the introgression of cultivated genotypes into the wild ones was not extensive. In the USA, wild beets have been reported along the California coast from San Francisco to San Diego (Carsner 1928, 1938). Carsner speculated that these were either *Beta maritima* or natural crosses between this species and the cultivated types. Wild beets have also been reported in the Imperial Valley of California; these have been classified as *Beta macrocarpa* and, perhaps,





**Fig. 5.2** Seed stalk with fully developed seeds of *Beta macrocarpa* (Martinez, California, USA)

crosses between *Beta macrocarpa* (Fig. 5.2) and cultivated beet (McFarlane 1975; Bartsch and Ellstrand 1999; Bartsch et al. 2003).

According to de Cauwer et al. (2010), around 40% of successful pollinations happen inside 15 meters from the pollen source. However, 2.5% of pollinations were detected some kilometers away. Although the general study of the pollen flow is very frequent in other anemophilous species, given the specificity of the single species, the best thing to do is to avoid generalizations and comparisons (de Cauwer et al. 2010).

The extensive genetic and genotypic variability among sea beet populations has been associated with the adaptability of the species under various conditions of environmental stress (Hanson and Wyse 1982). This enables sea beet to flower in inhospitable environments, often characterized by high salinity, limited water availability, and low soil fertility (Stevanato et al. 2001). In these environments, the wild populations are subjected to selection pressures very different from those present in beet cultivation. Faced with gene flow and the pressure of human activities in the areas colonized by sea beet, the genetic conservation of wild germplasm can be seen as securing a source of genetic resistance to biotic and abiotic stresses, to be used in future genetic improvement programs (Doney and Whitney 1990; Luterbacher et al. 1998; Frese et al. 2001). The ability of sea beet to hybridize with cultivated beet easily and without genetic abnormalities has facilitated a number of substantial improvements to commercial varieties. The phenomena of spontaneous intercrossing or gene flow from cultivated to wild poses a serious threat to the future conservation of the wild genetic resources (Bartsch et al. 2002), especially in the case of introduction of transgenic varieties (Bartsch and Schuphan 2002; Lelley et al. 2002).

Surveys carried out by Bartsch et al. (1999) helped to identify two alleles (Mdh2-1 and Aco1-2), normally present both in cultivated sugar beet and wild populations in the vicinity of areas devoted to commercial reproduction of seed. This evidence indicated interaction among the wild populations and commercial varieties. Crop-to-wild gene flow could reduce the native allelic diversity and introgress domesticated traits that lower fitness to environment into the wild populations (Arnaud et al. 2009). Such hybridization could lead to extinction of some sea beet populations, especially those located in environmentally challenging sites. Similar unfavorable gene exchange might happen through wild or feral beets, which grow between the cultivated crop and sea beets in some areas (Viard et al. 2004; Ellstrand et al. 2013).

As mentioned, beet crops have been selected for a biennial life cycle. Under certain conditions, plants (normally not exceeding 0.1% of the crop) can return to their ancestral state and flower in the first year. The seed produced by the bolted plants can give rise to weed beets. When this happens, the population gradually diverges from the original morphology, but even after many generations, does not approach the morphology of sea beet (Greene 1909; Ford-Lloyd and Hawkes 1986; Hanf 1990). Sometimes weed beets can originate from hybridization with sea beet or, rarely, with *Beta macrocarpa* (Lange et al. 1993; Bartsch et al. 2003). The effects of gene flow between wild and cultivated beets tend to homogenize the genetic variability in the populations, if not sufficiently isolated. This gene flow may be responsible for highly heterogeneous genotypes called “feral”, because they colonize sites affected by human activities (dams, ditches, street borders, etc.) outside of cultivated fields (Mücher et al. 2000). In many European countries, weed beets, mainly derived from bolted beets, can create difficulties for the beet crop because of their high competitiveness (Desplanque et al. 1999). Control of weed beets inside sugar beet fields using the usual herbicides is impossible because they are as sensitive as the beet crop. Only the use of transgenic resistant varieties is effective against weed beets (Coyette et al. 2005).

Gene flow via seed and pollen is an important process in plant evolution. Bartsch et al. (2003) and Viard et al. (2004) observed evidence of gene flow among sea beet, wild beet, and sugar beet, the sea beet located along the Northern France coasts, the sugar beet inland, the weed beet in between. In some sea beet populations and in weed beets in their vicinity, the presence of Owen CMS was detected, indicating that reciprocal crosses had occurred. Therefore, weed beet may be considered a bridge plant for gene flow between cultivated and sea beet. To avoid gene transfer between sea beet and crops and vice versa, it would be necessary to keep the isolation distance on the order of several kilometers (Viard et al. 2004). Evans and Weir (1981) observed an increased salt tolerance in annual weed beets, which could have resulted from pollen flow from the coastal *Beta*. Gene flow also can happen through seed dispersal, as was observed by Arnaud et al. (2003) (see chap. 3). To significantly minimize gene transfer between sea beet and crops and vice versa, it would be necessary to keep the isolation distance on the order of several hundred meters up to kilometers (Viard et al. 2004) or to establish management measures like bolter control.



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