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Carpobrotus edulis in Coastal California Plant Communities

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Introduction

The state of California is not an island surrounded by water, but the topography of the state creates an island-like setting for evolution. Mountains, desert and ocean surround California, all of which create effective barriers to dispersal. These barriers, and the heterogeneity of environments within the state, have led to a high degree of endemism. The mild climate of California also makes it exceptionally vulnerable to invasion by exotic species. Seventeen and one-half percent or 1025 species of the extant California flora are now exotic species (Rejmanek and Randall 1994). These numbers continue to increase as more and more species are both intentionally and inadvertently introduced into the state. California now also has a high number of species that are threatened as a direct result of these invasions by exotic plants (California Native Plant Society 1999).

Recent interest in restoration of the natural landscape has not skipped the California coastline. The high number of threatened and endangered endemic plant and animal species in California coastal plant communities, including species such as *Chorizanthe howellii* Goodm. (Howell's spineflower) and *Euphilotes battoides allyni* (El Segundo Blue Butterfly), has drawn specific attention to the need for restoring these communities, especially the dune and scrub communities (Dune and Prairie 1998, California Native Plant Society 1999). At many points along the shoreline, government, non-profit and local community groups have been attempting to restore coastal areas for recreational, aesthetic and ecological purposes. The major initial challenges are to acquire and protect this valuable land from development and to eradicate the myriad of invasive species, among them *Carpobrotus edulis*.

Carpobrotus edulis L. Bolus (Hottentot fig or South African ice plant) (*Aizoaceae*) is a succulent, mat-forming perennial plant from South Africa. It is believed to have been introduced into California in the early twentieth century (D'Antonio et al. 1993) or possibly even as early as the 1500s (BLM 2000). It was actively planted in the early 1900s as a means of stabilizing dunes, and more recently has been widely planted as a roadside ground cover by the California Department of Transportation (D'Antonio 1990, BLM 2000). It is also popular as an ornamental. It has dispersed from these plantings by means of both human and animal vectors. *C. edulis* has since been spreading from areas of cultivation into many native plant communities along the entire California coastline. These include active and stabilized dunes, grasslands, coastal scrub, bluff scrub, maritime chaparral and others (D'Antonio 1990). Coastal plant assemblages vary by community, and within the same communities may vary latitudinally, but they all seem to be susceptible to some degree of invasion by South African ice plant.

Carpobrotus edulis has incorporated itself into this variety of coastal plant communities through dispersal by herbivorous mammals (Vilà and D'Antonio 1998b). *C. edulis* appears to be most successful in mesic soil conditions, many of which are marine sand deposits (D'Antonio 1990), but in drier conditions may use CAM (crassulacean acid metabolism) photosynthesis (Schmalzer and Hinkle 1987). In these environments, *C. edulis* has managed to displace not only the putative native, non-invasive iceplant species, *Carpobrotus chilensis* L. (Sea Fig) but other native herbaceous plants, such as *Bromus carinatus* Hook & Arn. (California brome), *Abronia latifolia* Eschs. (Yellow sand verbena), *Artemesia pycnocephala* (Less.) DC. (Coastal sagewort, Beach sage), *Erigeron glaucus* Ker-Gawler (Seaside daisy),

Carex pansa L. (Bailey) (Sand-dune sedge), *Carex spissa* (L.) Bailey (San Diego sedge) and *Eschscholzia californica* Cham. (California poppy). It has also negatively affected native shrub species such as *Lupinus chamissonis* Eschs. (Silvery bush lupine, Dune bush lupine), *Ericameria ericoides* (Less.) Jepson (Mock heather, California heathgoldenrod), *Isocoma menziesii* (Hook & Arn.) Nesom var. *sedoides* (Greene) Nesom (White-flowered dune goldenbush) and *Artemesia californica* Less. (Coastal sagebrush) (D'Antonio and Mahall 1991).

Carpobrotus edulis is an extremely invasive plant species. It has been classified as an A-1 level exotic plant in the California Exotic Pest Plant Council's (CalEPPC) list of exotic plant pests of greatest ecological concern. An A-1 plant is described as one that is a most widespread and invasive wildland pest plant (California Exotic Pest Plant Council 1999). *C. edulis* is, as are most successful invaders, aggressive on several fronts. It can reproduce prolifically via sexual reproduction and can reproduce clonally (D'Antonio 1990, D'Antonio 1993). In addition, *C. edulis* has successfully hybridized with its native congener *Carpobrotus chilensis* (Vilà and D'Antonio 1998a). *C. edulis* can also create significant changes in resource availability for native species when present (D'Antonio and Mahall 1991). Finally, by its presence, *C. edulis* creates changes in the microclimate and disturbance regimes of some communities, effectively excluding some native species with specific climatic and disturbance cycle requirements (Mack and D'Antonio 1998, California Native Plant Society 1999).

In research conducted over a two-year period (1994-1995) at Bodega Bay Marine Reserve in northern California, Vilà and D'Antonio studied fruiting and seed dispersal (1998b) and clonal growth (1998a) of the two parental species of *Carpobrotus* (the congeners *edulis* and *chilensis*) and their hybrids. *Carpobrotus spp.* produce fleshy, fig-like fruits between February and September (D'Antonio 1993, Vilà and D'Antonio 1998b). Vilà and D'Antonio found that on average *C. edulis* and the hybrids bore substantially more fruit than *C. chilensis* (497, 366 and 13 respectively). The number of seeds per fruit was highest *in C. edulis*—three times higher than the other morphotypes—and the fruit quality (digestible biomass vs. non-digestible biomass) was highest in the hybrids (Vilà and D'Antonio 1998b).

Herbivores, including *Sylvilagus bachmanii* (Brush rabbit), *Lepus californicus* (Black-tailed jackrabbit), *Spermophilus beecheyi* (California ground squirrel) and *Odocoileus hemionus* (Mule deer) consumed fruits of *C. edulis* at a higher rate than those of *C. chilensis* (98.33% vs. 53.33% respectively) (D'Antonio 1990, Vilà and D'Antonio 1998b). Hybrid fruits were consumed at an intermediate rate (Vilà and D'Antonio 1998b). Vilà and D'Antonio also observed that there were fewer seeds of *C. chilensis* in herbivore scats than expected by fruit production. Because of this phenomenon and its softer seed coat, they postulated that *C. chilensis* seeds may be more often damaged by gut enzymes than those of the other two morphotypes (Vilà and D'Antonio 1998b). These factors (higher seeds per fruit, higher consumption of fruit and greater durability of seeds) combine to give *C. edulis* and its hybrids a significant reproductive and dispersive advantage over the native species, and therefore potentially greater fitness over multiple generations.

In studies of naturally growing clones, as well as transplanted cuttings of each morphotype in several different habitats, Vilà and D'Antonio (1998a) found that the hybrid clones survived, on average, better than either parent and that *C. edulis* survived better than *C. chilensis*. Coupled with the high rate of seed production and rate of dispersal, these results provide strong evidence of hybrid vigor resulting from *C. edulis* crossing with *C. chilensis*. The increased survival and growth of the clones of *C. edulis* and the hybrids, as well as their more successful sexual reproductive effort almost ensure the development of a greater seed bank for the invaders than the putative native (Vilà and D'Antonio 1998b). In uncontrolled conditions, the presence of a larger seed bank after a disturbance event could allow *C. edulis* to easily dominate habitats shared with *C. chilensis*. It is yet unclear exactly how the seed bank of *C. edulis* may affect other species in the variety of habitats in which it is found.

The invasibility of the various habitats along the California coast to *Carpobrotus edulis* seem to be related in part to their soil type, successional status, localized disturbances and herbivore community (D'Antonio 1993). For instance, active coastal front-dune is more easily invaded than mature coastal grassland. Once *C. edulis* becomes established, it may smother other species outright by forming deep, dense mats, or it may alter soil moisture content, stability or pH, making it difficult or impossible for other species to survive (D'Antonio and Mahall 1991, D'Antonio 1993, C. D'Antonio, personal communication). In the case of maritime chaparral, *C. edulis* can alter available space, nutrients and soil moisture for native species.

Although it seems to have difficulty initially becoming established in mature communities, *C. edulis* has become commonplace in maritime chaparral communities (D'Antonio et al. 1993). The reason is that it becomes dispersed into these chaparral communities by herbivores (through scat) after disturbance by fire. If the fire has been restricted to superficial soil areas, *C. edulis* may also germinate from deeply buried seeds in the seed bank. Chaparral is a fire-dependent system, which gives *C. edulis* ample opportunity to invade unless fire-suppression is occurring. The situation can become problematic for managers attempting to maintain a healthy chaparral system while eliminating or preventing establishment of *C. edulis*.

Once the non-native iceplant does become established, it can out-compete the native species for water, nutrients and space. In a study of root competition between *C. edulis* and *Haplopappus ericoides* and *H. venetus* [sic], D'Antonio and Mahall (1991) found that *C. edulis* significantly reduced soil moisture available for uptake by the other two species. In the presence of *C. edulis*, *H. ericoides* and *H. venetus* had altered rooting habits, growing deeper than they would in normal (*sans edulis*) conditions. The shrubs in areas where *C. edulis* had been removed also showed dramatic increases in growth (size and shape of canopy) and survival over time and in drought conditions versus control plants where *C. edulis* remained a competitor. They concluded that *C. edulis* was competing directly with the two shrub species for surface soil moisture (all three are shallowly rooted) and that it is possible that it was also competing for nutrients as well. This competition appears likely to reduce biomass, survival and reproduction of the native shrub species. In attempting to maintain or restore scrub communities, removal of *C. edulis* before onset of large-scale mortality of native shrubs becomes even more important in light of the fact that some native species do not develop seed banks (D'Antonio and Mahall 1991). If allowed to die off, these species may be particularly difficult to replace.

Options for Control

Carpobrotus edulis is an aggressive invader into many coastal systems, but it is not necessarily difficult to remove. Unlike many other invasive species, money is not the limiting factor in restorations involving iceplant removal. The limiting factors are largely time and manpower. Following are some iceplant removal techniques that can be used during coastal habitat restorations.

C. edulis can grow in mats 40-55 cm thick and 8-10 m wide per plant. It is also shallowly rooted (D'Antonio and Mahall 1991). Because of these factors, it is relatively easy to remove somewhat mature plants. They can be removed as if 'rolling up' a large carpet (D'Antonio 1993). The problem is largely a matter of contending with the large amount of biomass accumulated after removal. The volume and weight of iceplant can become extremely unwieldy if disposing of it off-site (L. Au, personal observation). In limited areas, if extensive planting is done shortly after removal and any new germination of *C. edulis* removed, restoration of a coastal community is feasible. In Monterey, efforts to restore coastal dunes involving manual removal of iceplant and over-planting with native species such as *Artemesia pycnocephala*,

Abronia latifolia and *Eschscholzia californica* have been more successful than expected (Jensen 1997).

In a restoration of Santa Barbara Island in Channel Islands National Park, two different species of iceplant (*Mesembryanthemum spp.*) were removed to encourage re-establishment of native plant communities. Part of the restoration area was cleared by hand and then tilled to encourage germination of seeds. New shoots were then removed and the area was planted and seeded with native plants. The restoration had mixed success because the *Mesembryanthemum* had significantly altered the soil chemistry–including salt level–of some of the sites, making it difficult for some plants to re-establish (D'Antonio et al. 1992). This type of removal and restoration would likely work very well with *Carpobrotus* because it grows in a similar way to *Mesembryanthemum*, but does not alter the pH and salt content of the soil to the same degree as *Mesembryanthemum spp.* (C. D'Antonio, personal communication). The drawback of all hand removal techniques are the limited spatial scales at which they can usually be applied because of time constraints and need to dispose of accumulated biomass. They are also labor intensive.

Removal of *C. edulis* can also be accomplished by using herbicides such as Round-up. In a restoration of coastal bluff grassland conducted over a 13-year period at Bodega Head, Bodega Bay in Sonoma County, hand applications of Round-up to areas heavily invaded by *C. edulis* allowed the restorers to retain healthy native plant communities and retard the spread of *C. edulis*. Only occasionally were they required to re-treat areas with the herbicide. After the iceplant was removed, native plants were able to recover without any additional human intervention (P. Connors, personal communication). This technique is comparable to hand removal in time and manpower requirements, but may be more efficient overall because of the lack of requirement for disposal of biomass. Manual removal techniques would be most efficient when there is negligible presence of native species.

In many locations, *Carpobrotus edulis* and hybrids co-occur with the putative native species *C. chilensis*. In areas where they co-occur, they often cover vast areas and it would be inefficient in terms of time and cost to try to remove the exotic plants exclusively by hand. In such areas, one option may be to rely on native herbivore species, such as brush rabbit and California ground squirrel to provide a competitive advantage to native species (D'Antonio 1993). Herbivores show a marked preference for the non-native species, acting as a significant cause of mortality for seedlings. By focusing on removal of fruiting plants and allowing the generalist herbivores to remove seedlings, ecologists (and others) could reduce competition by *C. edulis* against the native plant species (D'Antonio 1993). This practice would require a long restoration timeline because of the unlikelihood of being able to remove all fruiting plants before herbivore consumption and the need to wait for the seed bank to expire. It is also, as with any removal technique, labor and time intensive. It is unknown whether this technique has been used in any areas outside the study.

The final potential management technique for *Carpobrotus edulis* is the use of fire. After fire disturbance, *C. edulis* invades more easily but the seeds do not appear to be fire released (or heat germinated). On the contrary, *Carpobrotus* seeds cannot easily survive the temperatures of a brush fire. D'Antonio et al. (1993) found in laboratory studies that seeds were killed when soil temperatures exceeded 90ÚC for 5 minutes. Although soil heat conductivity is variable, it is likely that seeds near the soil surface would be destroyed in any high intensity fire. Instead, after fire there was rapid colonization by *C. edulis* in chaparral by dispersal from other sites in jackrabbit and deer scat. Before fire, *C. edulis* and other ground cover in chaparral was heavily browsed by brush rabbit, but afterward, brush rabbit

presence and browse was scarce because of increased distance from nearest cover after fire. As a result of these findings, D'Antonio et al. (1993) recommend a management technique of small, high intensity fires to control *C. edulis* establishment in chaparral. Although multiple small fires may not be the most efficient way to restore degraded chaparral, it may the most effective way to remove iceplant and prevent its return while restoring a fire-dependent community.

Conclusion

Carpobrotus edulis is an aggressive exotic species that has invaded the coastal plant communities of California. Like the putative native, *Carpobrotus chilensis*, it reproduces both sexually and clonally, spreading in ever-larger mats across the surface of the soil or sand. Unlike the native, *C. edulis* out-competes and in many cases, smothers other species, often creating near monocultures of itself over extensive areas. Restoration efforts involving iceplant removal currently seem to be concentrated in the south of the state, while many areas in the north are just beginning to address the problem. For instance, on the Samoa Peninsula in Humboldt County, *C. edulis* continues to spread and displace native plants (BLM 2000). This spreading habit can create great challenges for groups seeking to restore native habitat.

Groups from San Diego to Humboldt County in California have had to address the problem *of C. edulis* in restoring coastal dune, scrub, chaparral, etc. and find solutions appropriate to their topography and native plant communities. In areas dominated by fire dependent species, such as coastal scrub and chaparral, small, intense fires may be the answer. However, time, cost and available manpower may also preclude such an approach. In some cases, such as the dune restoration in Monterey, the solution may have been as simple as removing *C. edulis* from the surface of the sand and over-planting with native species. In other cases, the solutions are less apparent. The most time and cost effective approach for removal in most areas may be the use of chemical herbicides like Round-up. They are as effective as manual removal of the plants, and eliminate the disposal step required in manual removal.

In a state overrun by exotic species, *C. edulis* is apparently low on the priority list for California government control. Despite its listing by CalEPPC as a pest plant, *C. edulis* is still planted as an ornamental or ground cover (although to a lesser extent than years past) (BLM 2000) and it seems unlikely that it or its hybrids will disappear anytime soon. One possible future option may be the use of iceplant pathogens and scale insects as biological control agents. This option has likely not been greatly explored because of the continuing popularity of *C. edulis* as an ornamental (Schmalzer and Hinkle 1987). Any use of biological control agents would also need to be carefully controlled to prevent damage to the native species. For now, the greatest hope for control is that as interest in coastal restoration increases, more government agencies citizens and will become aware of the problem and help to address it by discontinuing its propagation, aiding in removal efforts and funding additional research on control techniques.

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Carpobrotus chilensis is a non-invasive species that grows in patches around existing vegetation. It is a putative native because it has been found in California since the 17th century but has never been documented in South Africa, where its congeners (*Carpobrotus spp.*) are native (Vilà and D'Antonio 1998).

Haplopappus ericoides and *H. venetus* var. *sedoides* have since been changed to *Ericameria ericoides* and *Isocoma menziesii* var. *sedoides*, respectively.