

Fitness of invasive *Carpobrotus* (Aizoaceae) hybrids in coastal California¹

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Abstract: Natural hybridization between previously allopatric plant species can produce highly successful lineages. We test the low-fitness-hybrid hypothesis in *Carpobrotus* and its implications for hybrid invasion. We examine reproductive fitness components of hybrids between the invasive non-native succulent *Carpobrotus edulis* (L. Bolus) and the non-invasive putative native *C. chilensis* (L.) from three populations in California coastal plant communities. Hybrids between the two species are very abundant and aggressive but it is not known if this is a transitory phenomenon. We find no support for the low-fitness-hybrid hypothesis in *Carpobrotus*. Fruit weight and seed set, mass and germination rate of hybrids were intermediate between or the same as a parental taxon. Survival, growth, and root to shoot ratio of hybrid seedlings did not differ from those of parental taxa. Although hybrid fitness is not superior to that of parental species, we believe that hybrids will continue to persist and invade California coastal communities because recruitment of seedlings did not differ from those of parental species. The highest survival probability of the introduced *C. edulis* may insure its successful invasion status compared to the putative native congener *C. chilensis*.

Keywords: allopatric species, *Carpobrotus*, hybrid fitness, interspecific hybridization, plant invasion.

Résumé: L'hybridation naturelle entre des espèces précédemment allopatriques peut engendrer une descendance très adaptée. Les auteurs ont voulu vérifier chez *Carpobrotus* l'hypothèse de la faible adaptation des hybrides et ses implications en ce qui concerne le pouvoir d'envahissement des hybrides. Pour ce faire, nous avons étudié les composantes du succès de reproduction des hybrides entre l'espèce exotique *Carpobrotus edulis* (L. Bolus) reconnue pour son fort pouvoir d'envahissement et l'espèce réputée indigène *C. chilensis* (L.), au pouvoir d'envahissement faible. L'étude a pris place au sein de trois populations de communautés végétales de la côte californienne. Les hybrides entre ces deux espèces sont très fréquents et agressifs, mais on ne sait pas si ce phénomène est transitoire. Les résultats de l'étude ne supportent pas l'hypothèse de la faible adaptation des hybrides chez *Carpobrotus*. Chez les hybrides, le poids des fruits, la production de semences, leur poids et leur taux de germination affichaient des valeurs intermédiaires comparativement aux valeurs des caractères correspondants chez les espèces parentales, ou encore des valeurs identiques à l'un ou l'autre des taxons parentaux. Chez les semis hybrides, la survie, de même que la croissance et le rapport racine sur tige ne différaient pas des valeurs pour les mêmes caractères chez les taxons parentaux. Bien que l'adaptation des hybrides n'était pas meilleure que celle des espèces parentales, on estime que les hybrides vont continuer de persister et d'envahir les communautés de la côte californienne puisque le taux d'établissement des semis hybrides ne différait pas celui des espèces parentales. La plus forte probabilité de survie de l'espèce introduite *C. edulis* pourrait lui assurer son succès en tant qu'espèce envahissante comparativement à l'espèce réputée indigène du même genre, *C. chilensis*.

Mots-clés: espèces allopatriques, *Carpobrotus*, adaptation des hybrides, hybridation interspécifique, envahissement des plantes.

Introduction

Natural interspecific hybridization has been recognized in all major plant groups and well studied floras (Stebbins & Ferlan, 1956; McArthur, Welch & Sanderson, 1988; Stace, 1991), and several authors have concluded that natural hybridization has played a major role in the reticulate evolution of plant taxa (Grant, 1971). Patterns of natural hybridization have been described among sympatric and parapatric closely related plant species (Epling, 1947; Levin & Smith, 1966; Adams & Kistler, 1991). Hybridization may also occur when two differentiated, and hitherto, geographically isolated species come into contact. The result can be low frequency occurrence of hybrid individuals (Marshall & Abbott, 1980), stable introgressant forms (Heiser, 1949) or aggressive, abundant hybrid genotypes (Thompson, 1991). An example of the latter situation is the almost complete

replacement of native cordgrass (*Spartina maritima* [Curtis-Fernald]) by an allopolyploid hybrid species, *S. anglica* after the introduction of northeastern American cordgrass, *Spartina alterniflora* (Loisel) to Great Britain. *Spartina alterniflora* is also invading the San Francisco Bay (California) and hybridizing with the native *S. foliosa*. These hybrids are recruiting and growing faster than the native *S. foliosa* (Daehler & Strong, 1997). However, the ecological and evolutionary mechanisms that lead to invasion of hybrids between previously allopatric species are poorly explored.

Several hypotheses have been proposed to describe how natural selection acts on hybrid individuals. Three hypotheses support low fitness of hybrids relative to parental populations: (i) the ephemeral hybrid zone hypothesis is consistent with the classical theory of speciation (Dobzhansky, 1970) and maintains that hybrids are unfit and therefore will not persist as a viable population; (ii) the dynamic-equilibrium hypothesis suggests that hybrids are maintained by a balance between dispersal and negative

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selection (Barton & Hewitt, 1985); (iii) the advancing wave hypothesis predicts that a parental species is spreading and hybrids are always at disadvantage (Campbell, Waser & Menéndez-Ackerman, 1997). In contrast, the bounded superiority model (Moore, 1977) predicts that hybrids have advantages over the parental individuals in certain habitats and will thus maintain viable populations in these sites. In a recent review of studies of hybridization in natural plant populations, Arnold & Hodges (1995) concluded that hybrids often have equivalent fitness to both parental taxa or greater fitness than at least one parental species. They suggest that more natural and experimental studies are needed to assess the consequences of hybridization.

Studies of plant hybrid fitness have focused on components associated with sexual reproduction and/or survivorship in response to biotic and abiotic ecological factors. Clearly, analyzing and coupling multiple components of fitness in different habitats may greatly contribute to understanding the evolutionary and ecological consequences of hybridization (Arnold & Hodges, 1995). For example, besides seed set, male fitness characters (pollen production) and post mating characters such as seed dispersal, seed germination, and seedling survival and growth are components of fitness (Primack & Kang, 1987) that are likely to contribute to the establishment and maintenance of hybrid individuals. Transplant field experiments to discern the ecological factors influencing the survival of hybrids and parental taxa are imperative for determining how selection acts on hybrid and parental taxa in nature.

Our objective is to examine fitness components of naturally occurring hybrid individuals in the genus *Carpobrotus* in California compared to putative parental species. Hybrids are the result of crossing between the invasive South African succulent *Carpobrotus edulis* (L. Bolus) and its congener *C. chilensis* (L.) in coastal plant communities. *Carpobrotus chilensis* is a putative California native species. Both *C. edulis* and hybrids are very abundant and aggressive, and hybrids occur in all habitats where either one or both parental species are found. Currently, we do not know whether hybridization is a transitory phenomenon in this group or whether hybrid individuals will continue to increase in abundance. High reproductive fitness of hybrids may be one of the key factors that determines successful invasion. Because hybrid individuals are very abundant in many sites (Albert, 1995) we believe that they have superior reproductive fitness compared to at least one of the parental species.

Material and methods

STUDY SPECIES AND SITES

Carpobrotus spp. (Aizoaceae) are perennial succulents easily recognized by their trailing habit and succulent, three-angled leaves and indehiscent fleshy fruits (Wisura & Glen, 1993). The perennial succulent *Carpobrotus edulis* (L. Bolus) (Aizoaceae) was introduced from South Africa to the Pacific coast of North America in the early 1900s for dune stabilization and erosion control. It has invaded a variety of coastal plant communities throughout California due to

effective fruit dispersal by native mammals (D'Antonio, 1990) and fast growth (D'Antonio, 1993). *Carpobrotus chilensis* (L.) is a non-invasive species that co-occurs in many of the same habitats as *C. edulis*. *Carpobrotus chilensis* appears to be unique to California but it is of unknown origin (Vivrette, pers. comm.). It has been in California at least since the 1600s (Bicknell & Mackey, 1988) and it is not present in the South African flora (Wissura & Glen, 1993). Intermediate morphotypes (hereafter hybrids) for leaf and flower characters between both species are present in several habitats such as backdunes, coastal bluff scrub, and grassland communities. Morphometric and isozyme analyses show that introgressive hybridization is taking place (Albert, D'Antonio & Schierenbeck, 1997; Gallagher, Schierenbeck & D'Antonio, 1997). More than 74% of individuals sampled along a series of coastal transects were classified as hybrids and relative ground cover of hybrid morphotypes is significantly higher than that of *C. chilensis* (Albert, 1995).

For our study we compared three morphotypes: the two parental species and hybrids. *Carpobrotus edulis* and hybrid morphotypes are invasive but *C. chilensis* is not. Selection of parental species followed descriptions by the Jepson manual (Hickman, 1993). Hybrids were chosen according to morphometric analysis (Albert, D'Antonio & Schierenbeck, 1997). These hybrids may belong to different genetic taxa (*F.* backcrosses, etc.) and seeds produced by both hybrids and parental species may not be pure hybrid or parental species, respectively. However, our objective was not to compare fitness of specific genetic taxa. Rather we were interested in comparing fitness between invasive (*C. edulis* and hybrids) and non-invasive *C. chilensis* morphotypes in natural pollination conditions where rampant hybridization is occurring.

We surveyed reproductive characteristics of *Carpobrotus* in three sites within coastal California: Manila Dunes (MD) (40° 52' N, 123° 54' W), Bodega Marine Reserve (BMR) (38° 19' N, 123° 4' W) and Morro Bay (MB) (35° 17' N, 120° 56' W). These sites all have the summer dry and winter-wet Mediterranean climate typical of California. Within each site individuals were sampled from populations containing both hybrids and parental morphotypes (Albert, 1995). The sampled populations at each locality were fewer than 500 m from the ocean. The MD and MB sites were in stabilized backdunes dominated by native shrubs and subshrubs, while the BMR site is a coastal bluff scrub on loamy-sand soil. Five fruits from each of ten plants per morphotype were collected from the three sites to compare fitness parameters among *Carpobrotus* morphotypes. To make sure that sampled plants were different individuals, each plant was at least 5 m away from any other sampled plant, with no dead *Carpobrotus* plants between sampled plants.

FRUIT AND SEED CHARACTERS

We randomly chose three fruits per plant and the number of seeds per fruit was estimated by counting the number of seeds in one carpel per fruit and multiplying for the number of carpels per fruit. We first checked if carpels within a fruit contained the same number of seeds by counting the

number of seeds in four carpels per fruit in 12 fruits of each type. The number of seeds per carpel within a fruit type showed little variation (one-way nested ANOVA, $F_{3,138} = 0.066$, $P = 0.98$). Fruits were oven-dried at 70°C until constant weight. Individual seed mass was obtained by weighing ten sets of 20 randomly selected dry seeds from two fruits of each plant. Weight of each set was divided by 20 to obtain mean weight for each plant.

SEED GERMINATION AND VIABILITY

The remaining two fruits per plant were selected for seed viability and germination analyses. Seeds were removed by squashing the fruits with a fork under running water. Seeds of the two fruits from the same plant were pooled. Forty randomly selected seeds from each plant were split into two groups of 20 and placed in two petri dishes containing washed sand under greenhouse conditions ($T = 25^{\circ}\text{C}$, 9 hours daylight). Seeds were checked once a week for 12 weeks and were considered to have germinated if both the radicle and cotyledons had emerged from the seed coat. Because of the small size of seeds and time constraints, only five seeds from each clone were tested for seed viability by the tetrazolium method. Seeds were soaked in 0.1% tetrazolium after piercing and soaking them in GA_3 400 ppm 4°C overnight (Ellis, Hong & Roberts, 1985).

SEEDLING SURVIVAL AND GROWTH AT BMR

Patterns of seedling abundance and distribution were impossible to assess in the field because seedlings are visually indistinguishable among morphotypes at the cotyledon and two leaf stage. Thus, seedling survival, growth and biomass allocation were compared using a seedling transplant experiment. Because of access and authorization problems this experiment was only conducted at BMR. In October 1994, seeds from one fruit from each of 15 plants per morphotype were pooled by morphotype. Seeds were spread in sand-filled trays which were placed in the BMR greenhouse in natural daylight conditions. Trays were watered with a mist system two minutes three times a day, 3 days per week. In January 1995, when seedlings had four true leaves, they were transplanted into a backdune and a coastal bluff scrub habitat. The coastal bluff scrub site is dominated by perennial species including *Eriophyllum staechadifolium* (Lag.) var. *artemisiaefolium* (Lagasca), *Erigeron glaucus* (Ker-Gawler) (Asteraceae) and *Bromus carinatus* (Hook & Arn.) and the annual grass species, *B. diandrus* (L.) (Poaceae) which cover the totality of the ground. In the backdune the most abundant species is *Ammophila arenaria* (L.) (Poaceae) which occupies 61% of total ground cover. Differences in the soil texture (loamy sand in the coastal bluff scrub and sandy in the backdune) may contribute to the lower water content of backdune (2.3%) soil compared to that in the coastal bluff scrub (6.8%) ($F_{2,12} = 55.01$, $P = 0.0001$; midday July 1995).

In each habitat, blocks containing six groups (two groups per morphotype) of seedlings (six seedlings per group) were planted. Within each block, one group of seedlings of each morphotype was selected at random and caged by chicken wire mesh to exclude vertebrate herbi-

vores. Seedling groups within a block were separated from each other by 2 m. Eight replicate blocks were installed at approximately 20 m intervals along a 160 m long transect. In the coastal bluff scrub, seedlings were planted within standing vegetation. In the backdune, seedlings were planted on open sand. Caging prevented herbivory from mule deer (*Odocoileus hemionus* [Colombianus]) and jackrabbit (*Lepus californicus* [Gray]), the most common vertebrate herbivores in our study site.

Seedling survival was counted several times during one year. In February 1996, two randomly selected seedlings per group were harvested. Roots were separated from shoots and oven-dried at 70°C until constant weight. Total biomass and root to shoot mass ratio was calculated as the average of the 2 selected seedlings. For data analysis, the mean of the eight average values per treatment was compared.

POLLEN VIABILITY

Pollen viability was tested in three flowers of ten clones per morphotype at BMR. More than 200 pollen grains were counted in each flower after staining with cotton blue (Hauser & Morrison, 1964). For data analysis, the average percentage of stained pollen grains per clone was compared.

STATISTICAL ANALYSIS

Fruit and seed characteristics were compared among the three morphotypes and among the three sites with a two-factor analysis of variance (ANOVA). When necessary, data were transformed to meet the assumptions of ANOVA. The Scheffé test was used for pairwise comparisons.

We compared survival of seedlings among morphotypes at the end of the BMR transplant experiment for each habitat by χ^2 -test. Heterogeneity in survival curves within an habitat were tested by the Gehan-Wilcoxon test (Pyke & Thompson, 1986; Fox, 1993). Total mean biomass and mean shoot/root mass ratio of seedlings were compared by an extension of the Kruskal-Wallis (H) test (Zar, 1984). Throughout this paper, means are shown (± 1 SE) unless otherwise indicated. Superanova (1989) and Statview (1992) were used for the computation of ANOVAs and survival analysis, respectively.

Results

FRUIT AND SEED CHARACTERS

Differences among *Carpobrotus* morphotypes in the components of fitness analyzed were site dependent (Figure 1). The interaction between site and morphotype was significant for fruit mass ($F_{2,81} = 3.49$, $P = 0.01$): hybrids were intermediate between putative parental taxa in all three localities (Scheffé test, $P < 0.001$), but in MB there were fewer differences between hybrids and *C. chilensis* individuals were in the other two sites. Fruits of *Carpobrotus edulis* had the greatest biomass and fruits of *C. chilensis* had the lowest (Figure 1).

For seed set there was a significant interaction between site and morphotype ($F_{2,81} = 3.03$, $P < 0.02$). Number of seeds per fruit of hybrids was intermediate between the parental taxa at MD (Scheffé test, $P < 0.001$), but in BMR and MB there were no significant differences between

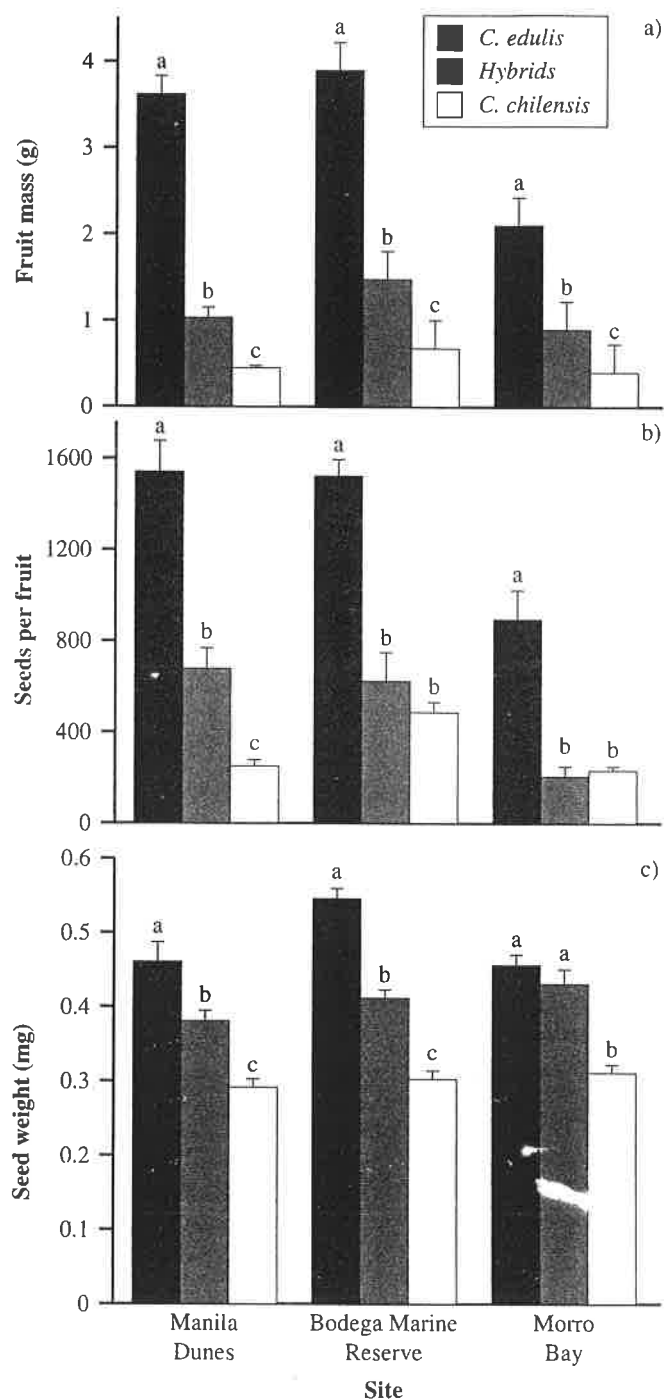


FIGURE 1. Female fecundity characters (mean \pm SE) of *Carpobrotus* morphotypes in Manila Dunes, Bodega Marine Reserve and Morro Bay: a) fruit weight, b) number of seeds per fruit, and c) seed weight. Bars with different lower-case letters show significant differences among morphotypes at a site.

hybrids and *C. chilensis* (Scheffé test, $P = 0.67$ in BMR and $P = 0.98$ in MB). Fruits of *C. edulis* bore more seeds than hybrid and *C. chilensis* morphotypes (Figure 1).

Seeds of the *Carpobrotus* taxa studied here are very small ($0.4 \text{ mg} \pm 0.01$, $n = 90$) and seed morphology differs among taxa. Seeds from *C. edulis* have a smooth coat and are oval in shape with the hilum located at the terminal

position. Seeds of *C. chilensis*, by contrast, have a wrinkled coat and are circular in shape with a protuberant hilum in a lateral position. Seeds from hybrid morphotypes have an intermediate morphology: the seed coat is smooth, and they are less oval than *C. edulis* seeds but the hilum, less protuberant than in *C. chilensis*, is located in a lateral position. Seed weight differed among morphotypes ($F_{2,81} = 0.01$, $P = 0.0001$), and was site dependent (Figure 1). In MD and BMR, seed mass from hybrid morphotypes was intermediate between the parental species (Scheffé test, $P < 0.001$). However, in MB, there were no significant differences between hybrids and *C. edulis* (Scheffé test, $P = 0.46$).

SEED GERMINATION AND VIABILITY

More than 80% of *C. chilensis* seeds from intact fruits germinated 3 months after seeding. However, germination of the other two morphotypes was less than 20% in MD and BMR (Figure 2). The interaction between the morphotype and locality was significant ($F_{4,81} = 3.43$, $P = 0.01$): in MD and MB germination of hybrids was intermediate (Scheffé test, $P < 0.001$). In BMR seed germination rates of hybrids were indistinguishable from those of *C. edulis* (Scheffé test, $P = 1$).

Seed viability was site and morphotype dependent ($F_{2,81} = 20.59$, $P = 0.0001$ and $F_{2,81} = 7.85$, $P < 0.0008$, respectively). Seeds from MD had lower viability ($43.33 \pm 4.6\%$) than those from BMR ($80.66 \pm 4.12\%$) and MB ($75.33 \pm 5.4\%$) (Scheffé test, $P < 0.001$). Hybrid seeds were less viable ($53.33 \pm 6.80\%$) than those of *C. chilensis* ($79.33 \pm 4.01\%$) (Scheffé test, $P = 0.004$), but not significantly different than *C. edulis* ($66.6 \pm 4.63\%$) (Scheffé test, $P = 0.47$). There were no significant differences in seed viability between parental taxa at different sites (Scheffé test, $P = 0.104$).

SEEDLING SURVIVAL AND GROWTH AT BMR

At the coastal bluff scrub, mean seedling survival time was less than two months (Table I). Four months after planting all seedlings, including caged ones, had died (Figure 3). The temporal pattern of survival was significantly different among uncaged morphotypes ($\chi^2 = 13.83$, $P = 0.001$, $df = 5$, Gehan-Wilcoxon test): *Carpobrotus chilensis* seedlings died faster than *C. edulis* ($\chi^2 = 14.35$, $P = 0.0002$, Gehan-Wilcoxon test). Uncaged *C. edulis* seedlings died faster than caged ones ($\chi^2 = 10.48$, $P = 0.001$, Gehan-Wilcoxon test).

TABLE I. Product-limit (Kaplan-Meyer) estimations of mean (\pm SE) survival time (days) of caged and uncaged *Carpobrotus* morphotypes planted at a coastal bluff scrub and in a backdune in Bodega Marine Reserve. Values followed by different lower-case letters are significantly different within an habitat (Gehan-Wilcoxon test)

	Caged	Uncaged
COASTAL BLUFF SCRUB		
<i>C. edulis</i>	57.02 \pm 1.98 ^a	49.21 \pm 1.58 ^b
Hybrids	56.25 \pm 2.52 ^a	56.60 \pm 3.18 ^{a, b}
<i>C. chilensis</i>	56.48 \pm 2.87 ^a	59.33 \pm 2.39 ^a
BACKDUNE		
<i>C. edulis</i>	239.22 \pm 21.08 ^a	147.62 \pm 10.49 ^b
Hybrids	212.81 \pm 19.39 ^a	156.54 \pm 16.28 ^b
<i>C. chilensis</i>	147.98 \pm 11.94 ^a	147.98 \pm 11.94 ^b

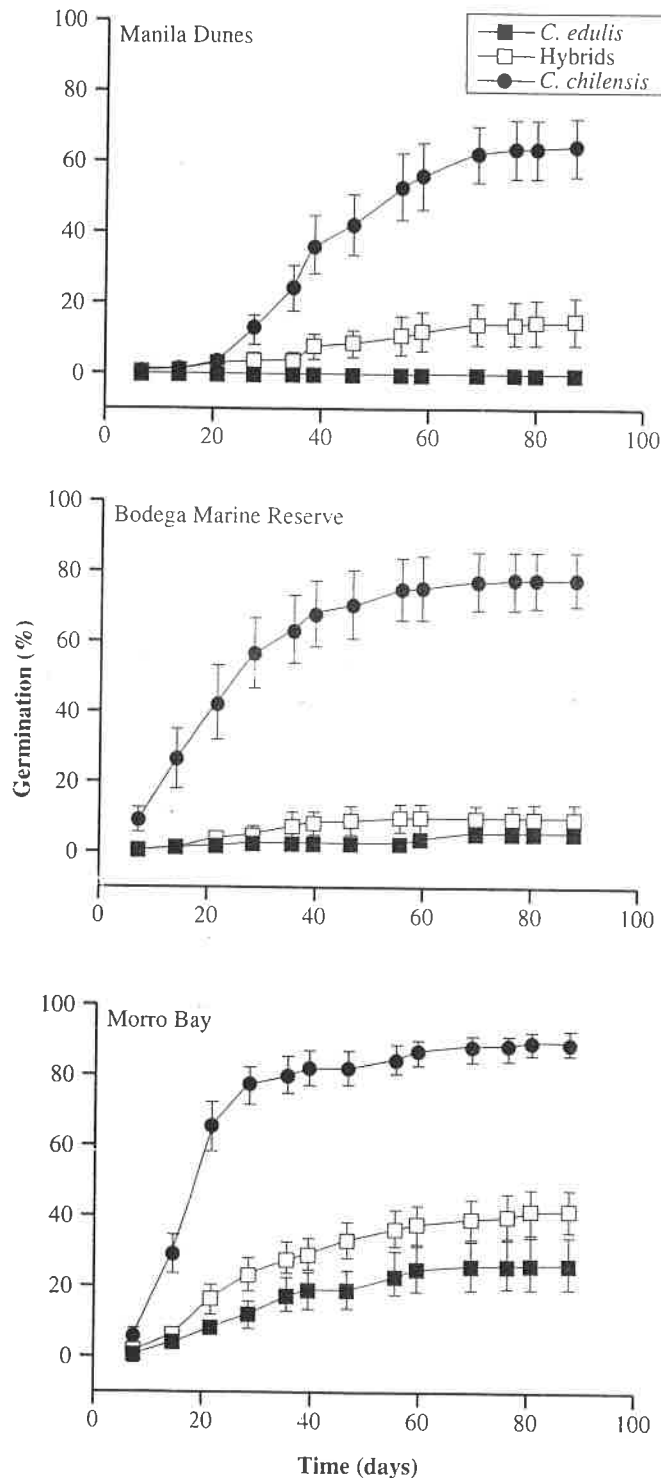


FIGURE 2. Germination rates (mean \pm SE) of *Carpobrotus* morphotype seeds from Manila Dunes, Bodega Marine Reserve and Morro Bay.

While the apparent source of mortality in the coastal bluff scrub was shading by annual grasses, in the backdune it was due to desiccation and phytophagous damage. In the backdune, mortality was highest before summer (from January to June) and tended to become progressively lower afterwards (Figure 3). The mean survival time ranged

from 5 to 8 months (Table I). The temporal pattern of survival was not significantly different among morphotypes ($\chi^2 = 7.62$, $P = 0.18$, $df = 5$, Gehan-Wilcoxon test). At the end of the experiment, 20% of seedlings survived. Caged seedlings had a higher survival rate (35%) than uncaged ones (10%) ($\chi^2 = 28.07$, $P = 0.0001$).

Total mass and root allocation of seedlings was not significantly different among morphotypes (Kruskall-Wallis test, $H = 4.78$ and $H = 0.38$, $P > 0.05$ respectively). Caging did not have a significant effect (Kruskall-Wallis test, $H = 2.43$ for total mass, $H = 3.23$ for root to shoot mass ratio, $P > 0.05$), (Table II).

POLLEN VIABILITY

Pollen viability was significantly different among morphotypes ($F_{2,27} = 10.09$, $P < 0.001$). Pollen from hybrid morphotypes showed a significantly lower percentage of stainable grains ($19.5 \pm 2.9\%$) than either parental species ($71.3 \pm 1.05\%$ *C. edulis*, $65.4 \pm 8.0\%$ *C. chilensis*). The difference between parental species was not significant (Scheffé test, $P > 0.05$).

Discussion

We found little evidence that hybrids were inferior to both parental species. For most of the characters that we measured, fitness of hybrids was intermediate between the two parents or equivalent to that of one of the parent species. Thus, we do not expect that the occurrence of hybrids will be a transitory phenomenon. Other studies have also rejected hybrid inferiority. Bennet & Grace (1990) found that hybrids were intermediate to parental taxa in the Louisiana *Iris* species complex in terms of ramet survival in response to manipulated shading conditions. Graham, Freeman & McArthur (1995) found *Artemisia tridentata* hybrids in Utah to have reproductive parameters equivalent to both parents.

The distribution and abundance of adult plants is also mediated by events that occur during seedling establishment. Habitat type and herbivory influenced *Carpobrotus* early seedling survival, but in our study there were no differences in survival rate between parental types and hybrids except for a slower mortality rate of uncaged *C. edulis* seedlings than *C. chilensis* in the coastal scrub. Seedlings did not survive long in the coastal bluff scrub regardless of the presence of cages. Mortality at this habitat may be due

TABLE II. Total biomass (g) and root to shoot mass ratio (mean \pm SE) of caged and uncaged *Carpobrotus* morphotypes planted at a backdune in Bodega Marine Reserve ($n = 8$). The effect of caging and morphotype was non significant (Kruskall-Wallis test, $p > 0.05$)

	Caged	Uncaged
TOTAL BIOMASS		
<i>C. edulis</i>	0.21 \pm 0.13	0.06 \pm 0.02
Hybrids	0.18 \pm 0.03	0.15 \pm 0.06
<i>C. chilensis</i>	0.17 \pm 0.07	0.06 \pm 0.01
ROOT TO SHOOT MASS RATIO		
<i>C. edulis</i>	0.18 \pm 0.03	0.27 \pm 0.02
Hybrids	0.21 \pm 0.02	0.20 \pm 0.03
<i>C. chilensis</i>	0.21 \pm 0.05	0.25 \pm 0.03

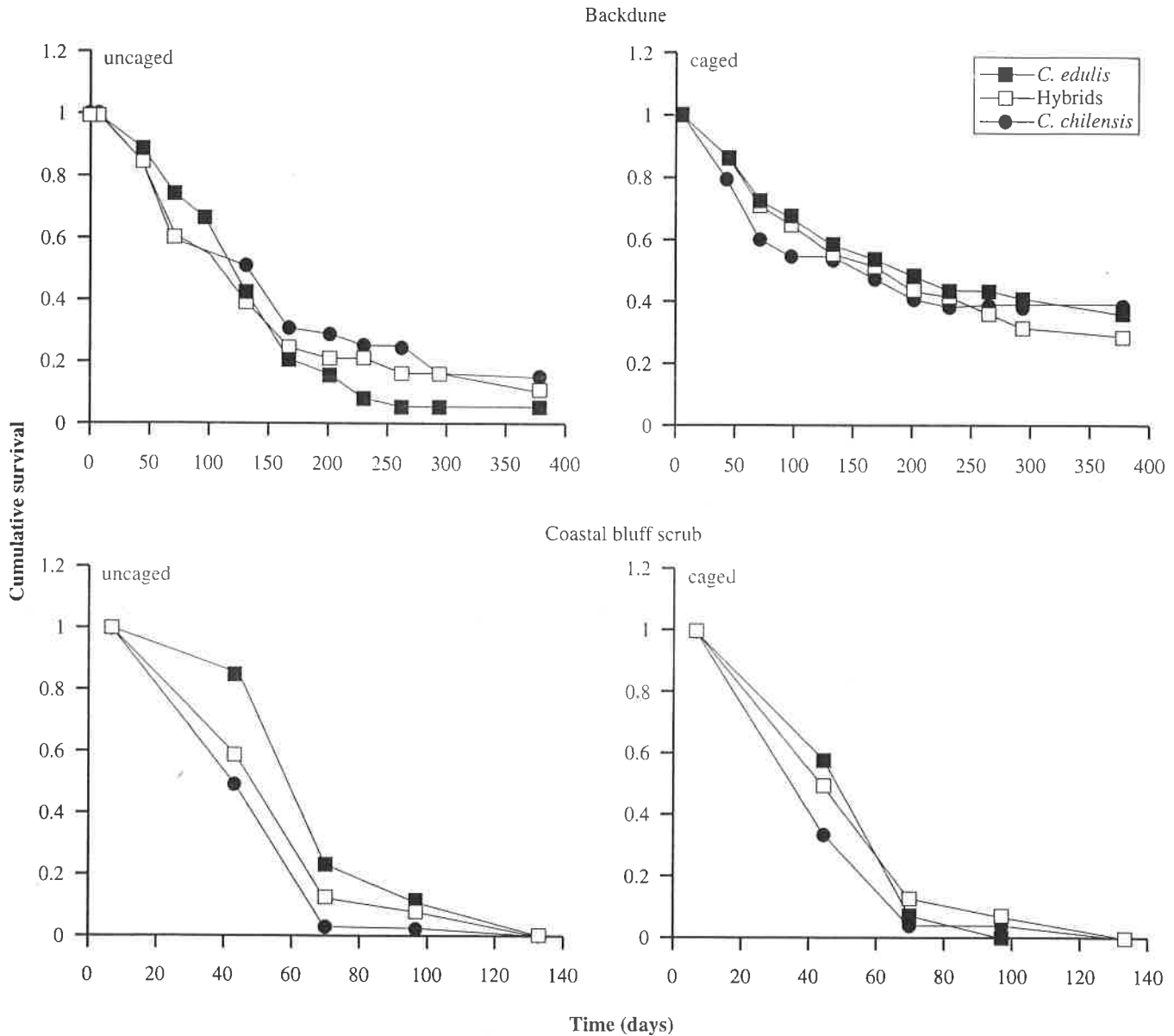


FIGURE 3. Seedling survivorship curves of *Carpobrotus* morphotypes from Bodega Marine Reserve in a coastal bluff scrub and in a backdune. Total initial number of seedlings per treatment = 48. Note differences in time scale between backdune and coastal bluff scrub.

to competition for light. Maximum mortality of seedlings took place before summer and after establishment and growth of the grasses *Bromus carinatus* and *B. diandrus*. D'Antonio (1993) found that in *C. edulis*, seedling establishment was reduced by neighboring vegetation including grasses and establishment only occurred on disturbed soil. In the backdune, survival was negatively affected by herbivory. D'Antonio (1993) also found *C. edulis* establishment to be negatively influenced by herbivory. In our study, some backdune seedlings also died due to physiological stress during summer and unknown phytophagous damage.

The lack of differences in seedling growth among morphotypes is likely to be the result of the short-term nature of this study. Seedling growth of *Carpobrotus* is slow for the first year under field conditions (D'Antonio, 1993) and it may not be until larger sizes that growth differences among

morphotypes are expressed. Comparative growth studies of cuttings show that hybrids and *C. edulis* attain significantly more biomass than *C. chilensis* plants within one year and are more resistant to mammal herbivory (Vilà & D'Antonio, in press). Resistance or tolerance to herbivory may lead to successful invasion by non-native species. Simoes & Baruch (1991) found that the introduced grass *Hyparrhenia rufa* compensated for defoliation by increasing tillering and higher leaf growth rate compared to the native grass *Trachypogon plumosus*. Similarly, Schierenbeck, Mack & Sharitz (1994) found that the introduced woody vine *Lonicera japonica* accumulated aboveground biomass as a compensatory response to herbivory, while the native *L. sempervirens* was damaged by both insect and mammal herbivory. Thus, response to herbivory can reinforce superiority of introduced species and hybrids in some habitats compared to native species.

In a previous study we have also found that fruit consumption and seed dispersal are selective forces on hybrid genotypes (Vilà & D'Antonio, 1998). Hybrid and *C. edulis* seeds are dispersed more than *C. chilensis*. Thus, although in this paper we only report some reproductive parameters to estimate hybrid fitness, exogenous ecological factors mediated by biological interactions, *i.e.*, herbivory and dispersal, reinforce hybrid success over *C. chilensis*.

The site dependence of hybrid fitness as measured by seed set, weight, viability and germination may reflect genetic differences between the hybrid populations at the different sites or responses to differences in the biotic and abiotic environment at each site. Hybrid fitness depends on genotypic class (*i.e.*, F_1 , backcross) (Arnold & Hodges, 1995). Potts (1986) found that although F_1 *Eucalyptus* hybrids between *E. risdonii* and *E. amygdalina* had lower values for reproductive parameters than parental taxa, backcrossed individuals had intermediate reproductive fitness compared to parental taxa. We do not know what the genetic status (F_1 , F_2 , or backcrossed) of any of our hybrid samples was. However, both morphological and isozyme data suggest that backcrossing does occur particularly in the direction of *C. edulis* (Albert, D'Antonio & Schierenbeck, 1997; Gallagher, Schierenbeck & D'Antonio, 1997). Genetic studies are needed to determine fitness of F_1 versus backcrossed *Carpobrotus* individuals in our study region. Schierenbeck *et al.* (unpubl.) are currently analyzing nuclear and chloroplast markers to assess the abundance of introgressed individuals in California *Carpobrotus* species. However, our objective was to determine fitness of those intermediate-like morphotypes that matched the description of invasive hybrid morphotypes (Albert, 1995), rather than to determine fitness of specific hybrid taxa.

Plant fitness is also dependent on the success of pollen in fertilizing ovules. Our results show that for *Carpobrotus* the pollen quality of hybrid morphotypes is lower than the parental morphotypes in at least one site. This pattern is consistent with other plant hybridization studies. Love & Feigen (1978) found that putative hybrids between the introduced *Crataegus monogyna* and the native *C. douglasii* produced less viable pollen than the putative parental taxa. However, as shown in *Helianthus* hybridization in North America, low pollen fertility (Heiser, 1947) is not indicative of low frequencies of hybridization and reticulate evolution can still occur (Rieseberg, 1991). Thus, low pollen viability in *Carpobrotus* hybrids does not necessarily determine low hybrid fitness. Moreover, indirect methods of male fertility such as the one used in our study do not necessarily give accurate results. Staining is affected by pollen ontogeny and quality (*e.g.*, old or dry pollen samples may be faintly or not at all blue) and environmental factors (Kearns & Inouye, 1993). Some faintly blue pollen grains had not been counted as fertile.

Fitness is not only a function of seed production (Bergelson, 1994) but of the likelihood of offspring establishment which depends on successful dispersal, germination, and seedling survival (Primack & Kang, 1987). Figure 4 illustrates the probability of a seed in a ripe fruit becoming an established 1st-year seedling, and the number of seeds per plant that might successfully become seedlings through the different stages of the reproductive cycle for

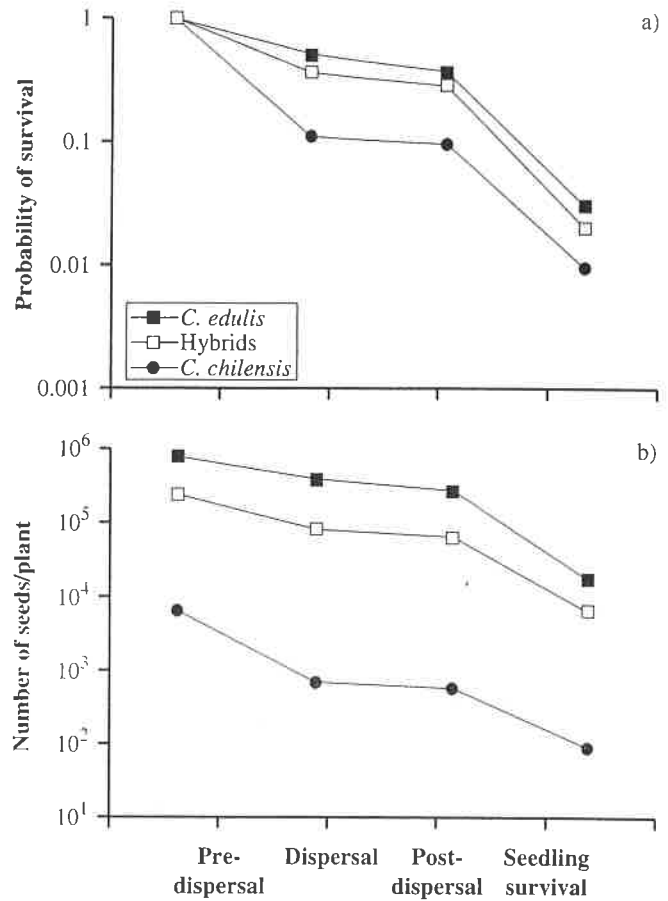


FIGURE 4. Recruitment expectancies of 1st-year *Carpobrotus* seedlings at a backdune in Bodega Marine Reserve. a) Probability of survival throughout each recruitment stage. b) Decline of the number of seeds per plant that will become seedlings throughout the recruitment process. Pre-dispersal = number of seeds per plant; Dispersal = proportion of seeds in scats, these values were obtained in a previous study (Vilà & D'Antonio, 1998); Post-dispersal = seed viability; Seedling survival = seedling survival one year after transplanting. Pre-dispersal probabilities were arbitrarily set at 1.0. Note log-scale.

Carpobrotus in the backdune at BMR for the period 1995-1996. For this purpose, we assumed that successive transition probabilities were independent and that the probability of a seed reaching recruitment can be estimated as the product of the previous elemental transition probabilities (Gill & Marks, 1991; Herrera *et al.*, 1994). To estimate this probability of survival, additional data from BMR in 1994 was collected and is published elsewhere (Vilà & D'Antonio, 1998). We chose an estimation of the number of seeds per plant as the pre-dispersal stage, the proportion of seeds per morphotype in the main frugivore (*Odocoileus hemionus* [Colombianus] and *Lepus californicus* [Gray]) scats as the dispersal stage, the viability of seeds as the postdispersal stage and survival of uncaged seedlings in the backdune as the recruitment stage. This crude estimation of final *Carpobrotus* fitness shows that only 3%, 2% and 1% of initial seed set from *C. edulis*, hybrids and *C. chilensis*, respectively, might become established 1st-year seedlings. According to our simple model, in this habitat hybrids would have 2.6 times fewer 1 year seedlings than *C. edulis*, but 28.2 times more than *C. chilensis*.

In conclusion, for the *Carpobrotus* spp. system studied, we do not accept that hybrids have lower fitness than parental species (ephemeral hybrid zone hypothesis, dynamic-equilibrium hypothesis and advancing wave hypothesis). Although recruitment probability of hybrids is not superior to both parental species, we can not reject the bounded superiority hypothesis because hybrid fitness is closer to the invasive *C. edulis* than to the non-invasive *C. chilensis*. Hybrid seed number per plant is lower than for *C. edulis*. However, low seed production is not a good predictor of invasiveness (Bergelson, 1994). Other intrinsic (*i.e.*, clonal growth) and extrinsic (*i.e.*, seed dispersal, herbivory) factors than the production of seeds can contribute to the invasiveness of hybridizing *Carpobrotus* in coastal California.

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