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## HYBRID VIGOR FOR CLONAL GROWTH IN *CARPOBROTUS* (AIZOACEAE) IN COASTAL CALIFORNIA

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**Abstract.** One of the consequences of the human-caused movement of plant species around the globe is hybridization between previously allopatric species. Introgressive hybridization between the non-native, invasive perennial succulent *Carpobrotus edulis* and the putative native, non-invasive *C. chilensis* is occurring throughout coastal California, leading to a high abundance of aggressive hybrid morphotypes and the loss of open space for native species establishment and growth. We test the hypothesis that hybrid vigor for vegetative growth and resistance to herbivory contributes to successful invasion by hybrid morphotypes. We compared survival and vegetative growth of transplanted cuttings of three morphotypes (parental species and hybrids) in three habitats in a factorial watering and caging experiment. Overall *Carpobrotus* growth was both water and herbivore limited. Hybrids displayed higher growth than either parental species. Hybrids always had higher survival in response to herbivory than *C. chilensis*, but survived better than *C. edulis* only in the bluff scrub. Growth of hybrids was higher than *C. chilensis* in the backdune and grassland but only higher than *C. edulis* in the backdune. *Carpobrotus chilensis* had the lowest survival to herbivory and the slowest growth. Our data suggest that greater resistance to mammalian herbivory coupled with hybrid vigor for vegetative growth can contribute to the invasive status of hybrids. High susceptibility to browsing and slow growth of *C. chilensis* at least partially explain its non-aggressive nature in coastal California.

**Key words:** biological invasion; clonal growth; exotic species; hybrid superiority; mammalian herbivory.

### INTRODUCTION

Hybridization between previously allopatric species has been recognized as one of the consequences of anthropogenic movement of species around the globe. Hybridization between native and introduced species has the potential to dilute the gene pool of native species and create highly aggressive genotypes that may be undesirable in terms of management for native species (Ellstrand 1992, Rhymer and Simberloff 1996). However, the role of hybridization in plant invasion has been understudied. Hybridization has been suggested to be a factor that allows the spread of plant species into areas they did not previously occupy (Abbott 1992). For example, the shrub *Lantana camara* was produced in cultivation through hybridization and is now an aggressive pest in many countries (Holm et al. 1970). The allopolyploid *Spartina anglica*, which resulted from hybridization between the non-native *S. alterniflora* and the native *S. maritima*, has invaded salt marshes throughout England, where it has become a dominant species (Thompson 1991). Hybrid vigor for

vegetative growth may be one of the reasons for displacement of parental morphotypes or native species.

Three main hypotheses have been proposed to explain the occurrence of hybrids that assume different levels of fitness for hybrids compared to parents (Arnold 1992, Harrison 1993). The bounded hybrid superiority hypothesis assumes that fitness of hybrids will be superior to parental populations only in certain habitats (Moore 1977). In contrast, the ephemeral hybrid zone hypothesis (Dobzhansky 1970) and the dynamic equilibrium model (Barton and Hewitt 1985) assume lower fitness of hybrids than either parental taxon, regardless of habitat. Because plant hybrid vigor is caused by the interaction of genes, metabolism and environment (Sinha and Khanna 1975, Frankel 1983), the performance of hybrids must be observed in multiple environments in order to understand the ecological and evolutionary implications of hybridization. There are several examples of plant hybrids showing higher fitness than putative parents in certain ecological conditions (Bennet and Grace 1990, Arnold and Hodges 1995, Graham et al. 1995). In most studies, fitness is measured in terms of reproductive parameters or survival, or both, but few studies have explored clonal growth (Emms and Arnold 1997). In addition, some investigators have found that hybrid individuals are more resistant to herbivores than parental species (e.g.,

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TABLE 1. Characteristics of the three study habitats in Bodega Marine Reserve in northern California.

	Backdune	Bluff scrub	Coastal grassland
Vegetation	perennials†	perennials, annual grasses, and forbs‡	annual grasses§
Ground cover (%)	60.6	>100	>100
Soil texture	sand	loamy sand	loamy sand
Soil H <sub>2</sub> O content (%)	2.3 ± 0.5	6.8 ± 1.0	7.2 ± 1.2
pH	8.16	6.91	5.64
C:N ratio	11.33	11.81	11.14
Total C (mg/g)	0.14	3.85	2.84

† *Ammophila arenaria*.

‡ *Eriophyllum staechadifolium* Lag. var. *artemisiaefolium*, *Erigeron glaucus*, *Bromus diandrus*, *B. carinatus*, *Camissonia thifolia*.

§ *Bromus diandrus*, *B. carinatus*, *Holcus lanatus*, *Lupinus arboreus*.

|| Mean ± 1 SE in July 1995.

Boecklen and Spellenberg 1990), which may result in higher fitness. By contrast, other studies have found that hybrids have higher (e.g., Whitman et al. 1994), the same, or intermediate (Fritz et al. 1994) susceptibility to herbivory than parental populations. The least likely outcome is that hybrids are attacked less than parental taxa (Strauss 1994). High resistance to herbivory may be an extrinsic cause of hybrid vigor and spread of hybrids.

In perennial clonal plants, fitness is difficult to assess because it depends on both sexual reproduction and ramet production. Clearly, ramet production contributes to decreased genet senescence, and consequently it increases plant fecundity (Eriksson 1993). Furthermore, clonal growth increases ground cover and decreases space availability to the establishment and growth of other species. In clonal plants the occurrence and expression of hybrid vigor remain largely unexplored.

*Carpobrotus edulis* L. Bolus (Aizoaceae) is an aggressive exotic perennial that is considered a widespread, invasive wildland pest plant in coastal California where it displaces native plants (Anderson et al. 1996). It co-occurs with its non-invasive, possibly native congener, *C. chilensis* L. Natural hybridization and introgression between species is occurring (Albert et al. 1997, Gallagher et al. 1997). It is not clear what factors limit the distribution and abundance of *C. chilensis* or hybrid forms, yet hybrid forms are very common and are widely distributed. Many hybrid clones have high ground cover and are associated with low numbers and low cover of native species within their boundaries (Albert 1995a). Thus hybrids may be at least as much of a management problem as *C. edulis*, but their potential for vegetative growth has not been studied. They are not currently listed explicitly as a management problem taxa by the California Exotic Pest Plant Council.

Here we compare clonal growth and vegetative performance between hybrid and parental morphotypes. We use a cutting transplant experiment in three different plant communities representing a range of environments over which these species are found (Albert

1995a). Further, we test whether hybrid performance relative to parents is affected by water availability or resistance to herbivory. We specifically address the following questions: (1) Do hybrid morphotypes have a higher relative clonal growth rate than putative parental taxa? (2) Are hybrid morphotypes less damaged by herbivores than putative parental taxa? (3) Does water limitation affect the relative performance of hybrids and parental morphotypes? (4) How do patterns of survival and growth of all taxa differ among habitats?

## MATERIALS AND METHODS

### Study sites and species description

The study was carried out in Bodega Bay Marine Reserve in northern California (38°19' N, 123°4' W) during 1994 and 1995. The climate is Mediterranean; mean daily temperatures range from 9.2°C in January to 13.4°C in August. The annual precipitation of 773 mm falls largely between November and April. Previous morphometric analyses found that both putative parental populations and hybrid morphotypes co-occur in the area (Albert et al. 1997). The study was carried out in three different habitats: a backdune, a bluff scrub, and a coastal grassland. In the backdune, the most abundant plant species is *Ammophila arenaria* L. (Poaceae), which occupies 61% of total ground cover. The bluff scrub is dominated by perennial shrubs including *Eriophyllum staechadifolium* Lag. var. *artemisiaefolium* Lagasca and *Erigeron glaucus* Ker-Gawler (Asteraceae), the perennial grass *Bromus carinatus* Hook & Arn (Poaceae), and the annual grass *B. diandrus* L. These two grasses are the dominant species in the grassland. Differences in total carbon and soil texture (pure sand in the backdune vs. loamy sand in the bluff scrub and grassland) may have been the cause of lower water content in backdune soils compared to the other two habitats ( $F_{2,12} = 55.01$ ,  $P = 0.0001$ ) in July 1995 (Table 1). Soil pH ranges from neutral at the bluff scrub to moderately acid in the coastal grassland (Table 1).

*Carpobrotus* spp. (Aizoaceae) are perennial succulents easily recognized by their trailing habit and suc-

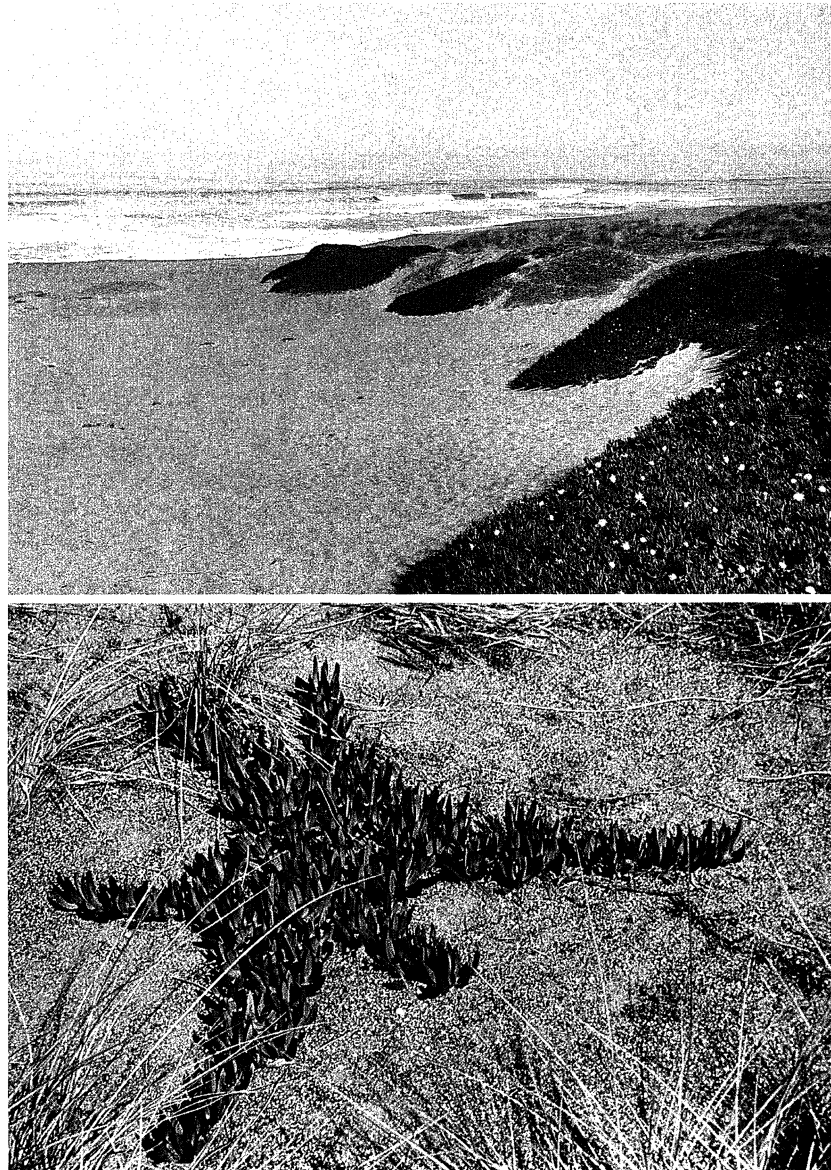


PLATE 1. Clones of the non-native succulent *Carpobrotus edulis* and hybrids between *C. edulis* and the putative native *C. chilensis* are invading backdune communities in northern California (top). Hybrids (bottom) have a vigorous clonal growth that increases the invasive status of *Carpobrotus* in coastal California.

culent triangular leaves. Stems root at the nodes as they spread. They have indehiscent fleshy fruits with a sweet aroma (Wisura and Glen 1993). *Carpobrotus edulis* was introduced to California from South Africa in the early 1900s for soil stabilization, and has been widely planted along roadsides and railroad tracks. It has invaded coastal communities through vertebrate seed dispersal (D'Antonio 1990) and rapid clonal growth (D'Antonio 1993). Invasion of coastal communities by *C. edulis* is limited by both herbivory and physical factors (D'Antonio 1993, D'Antonio et al. 1993). Physical factors are particularly important in dune environments, while herbivory is of overriding importance in bluff

scrub sites (D'Antonio 1993). The non-invasive *C. chilensis* grows as sparse patches of long, thin branches intermingled with the other vegetation. There is no information about ecological factors that influence its performance. *Carpobrotus chilensis* appears to be unique to California, but it is of unknown origin (N. Vivrette, *personal communication*). It has been in California at least since the 1600s (Bicknell and Mackey 1988), and it is not present in the South African flora where *Carpobrotus* spp. are native (Wisura and Glen 1993).

According to morphometric (Albert et al. 1997) and isozyme analyses (Gallagher et al. 1997), *C. edulis* and

*C. chilensis* appear to be hybridizing and backcrossing with *C. edulis* individuals. Hybrid derivatives (hereafter, hybrid morphotypes) are intermediate to parental morphotypes for various vegetative and reproductive characters with leaf length/leaf width, keel serration, fruit diameter, and number of carpels (Albert et al. 1997) being the most distinctive characters. These characters, along with flower color and size, were used to recognize hybrids and parental species in the field. *Carpobrotus edulis* flowers are yellow and those of *C. chilensis* are magenta. Hybrids have pink or magenta corollas with intermediate diameter compared to parental flowers ( $76.5 \pm 1.8$  for *C. edulis*,  $65.7 \pm 2.7$  for hybrids, and  $47.8 \pm 1.0$  for *C. chilensis* [mean  $\pm 1$  SE]). Both *C. edulis* and hybrid morphotypes have a dense mat-like growth form while *C. chilensis* mats are shallower in depth and have more bare space within them (Albert 1995a). Here we employ hybrids of intermediate appearance, *C. chilensis* and *C. edulis*.

#### *Growth of naturally occurring plants*

In May 1994, three branches within each of 20 clones of *C. chilensis* and hybrid morphotypes and 15 clones of *C. edulis* were tagged in the bluff scrub habitat. The length of the branch was measured above the marked node. The same procedure was followed for 20 clones of *C. chilensis* and hybrid morphotypes in the backdune. *Carpobrotus edulis* clones were not present in this habitat. No clones were marked in the grassland area because very few of any type were present. *Carpobrotus edulis* individuals have been actively removed from this habitat by Bodega Bay Marine Reserve managers. Morphotypes were recognized according to the above-mentioned leaf and flower characters.

In April 1995, branches were harvested. The length of the main and all secondary branches was measured to the nearest centimeter. In order to take initial among-branch variation into account, branch growth was expressed as the incremental increase over the initial branch length. The relative increase in total branch length (hereafter, stem length) was calculated as  $S_{t_1} - S_{t_0}/S_{t_0}$ , where  $S_{t_1}$  = length (sum of main and secondary branches) at the harvesting time and  $S_{t_0}$  = length at time of tagging. Stem length was averaged among the three branches within each clone. Differences among the three morphotypes were examined with ANOVA for the bluff scrub plants. Differences between *C. chilensis* and hybrid morphotypes in both the bluff scrub and backdune were analyzed by a two-factor ANOVA after  $(\ln + 2)$  transformation.

#### *Transplant experiment*

Vegetative growth of *C. edulis*, *C. chilensis*, and their hybrid derivatives was compared under different ecological conditions by transplanting cuttings into the backdune, bluff scrub, and coastal grassland at Bodega Marine Reserve. To minimize ecotypic variation, cuttings were selected from only one habitat, the bluff

scrub. Cuttings were selected from individuals matching descriptions of parental species (Hickman 1993, Albert et al. 1997) or hybrids (Albert et al. 1997). The three categories (each species plus hybrids) will be referred to as morphotypes. Although the exact genotypes in this study were not known, morphometric analyses suggested that selected hybrids may belong to F1 taxa (Albert et al. 1997). However, our objective was not to compare growth among *Carpobrotus* spp. genotypes but to compare growth between invasive and non-invasive morphotypes.

Ten cuttings were taken from 20 clones of each morphotype, but only 168 cuttings of each morphotype were used in the transplant experiment. Each cutting had between 2 and 5 nodes and was <20 cm long when collected in March 1994. The number of leaves and nodes, length, and fresh mass were recorded for each cutting. Cuttings were planted into sand in the Bodega Marine Reserve greenhouse. Approximately one month later when rooting had occurred, cuttings of a given morphotype were combined into one pool from which 56 individuals per morphotype were randomly chosen for each planting habitat. In each habitat, cuttings were planted into blocks of 4 cuttings per morphotype, with a total of 12 cuttings in one block. All cuttings within a block were planted at least 2 m from their nearest cutting neighbor, and natural vegetation was not disturbed when cuttings were planted. Each of the cuttings within a morphotype was then randomly assigned to one of the following treatments: (1) with cage, no supplemental water; (2) with cage and supplemental water; (3) without cage, no supplemental water; and (4) without cage, supplemental water added. Blocks were replicated 14 times within a habitat, and each block was 5 m from an adjacent one. Thus 504 cuttings were planted in total. Cages were made with  $1 \times 0.4 \times 0.4$  m chicken wire meshing (2.5 cm) and had a top to prevent grazing by mule deer (*Odocoileus hemionus* Columbianus) and jackrabbit (*Lepus californicus* Gray).

All cuttings were watered when planted and again one week later with an amount corresponding to 16 mm of precipitation each time. After that time, only cuttings assigned to supplemental water treatments were watered. Watering occurred weekly in June 1994, and from the last week of August through the end of September of 1994. The total supplement of water for a cutting corresponded to 304.85 mm precipitation.

In May 1995 we recorded mortality of cuttings in all three habitats and harvested all living cuttings. The total length of the main and secondary branches was measured to the nearest centimeter, and cuttings were weighed. A subset of cuttings was then dried. Dry mass (forced-air oven dried at 90°C to constant mass) was related to fresh mass by the following equation:

$$\text{Dry mass} = 0.124 + 0.102(\text{fresh mass})$$

( $n = 90$ ,  $r^2 = 0.92$ ). This equation was obtained by

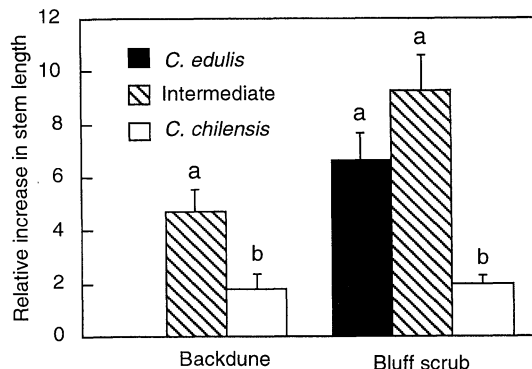


FIG. 1. Relative increase ( $[S_{t_1} - S_{t_0}]/S_{t_0}$ ) in stem length in a 1-yr period of naturally occurring *Carpobrotus* morphotypes in a backdune and bluff scrub at Bodega Marine Reserve. Bars indicate mean of the average of three tagged branches + 1 SE. Significant differences among morphotypes within a habitat are indicated by different lowercase letters.

weighing 30 fresh cuttings of each morphotype, drying them, and reweighing them. No significant differences were found among morphotypes ( $F_{2,84} = 0.16$ ,  $P = 0.85$ ), so all data were combined to obtain the final regression.

Because of the amount of work involved and the disturbance created by root excavation, only roots of cuttings in the backdune (where the soil is easily excavated and disturbance to native plants was minimal) were harvested. Root biomass was obtained after drying washed roots at 90°C until constant mass was achieved. Stem length and relative biomass increase (hereafter, relative growth) was calculated as described above for naturally occurring plants.

#### Data analysis for transplant experiment

Cutting mortality was analyzed as percentage of original cuttings that died during the experiment using a loglinear model (GLIM), considering the error as binomial (Crawley 1993). Loglinear models are used to analyze contingency tables with three or more dimensions (Zar 1984). In our study, the loglinear model allowed us to compare how the observed cutting survival data was affected by habitat, morphotype, watering, caging, and the combination of these variables.

Differences in stem length and relative growth were tested by ANOVA. Because of missing cells in the experimental design, we could not include all treatment combinations into the model (randomized unbalanced block design) (Shaw and Mitchell-Olds 1993). For this reason, we performed two ANOVAs within each habitat. The first ANOVA compared differences between *C. edulis* and hybrid morphotypes in all four treatment combinations (three-way unbalanced ANOVA with morphotype, caging, and watering as fixed effects). Survival of uncaged *C. chilensis* cuttings was frequently zero, so *C. chilensis* could not be included in this analysis. The second ANOVA included only caged cuttings from all three morphotypes (two-way unbalanced

ANOVA with morphotype and watering as fixed effects). Pairwise comparisons of means among morphotypes were done when ANOVAs indicated significant effects. Data were log transformed before analysis ( $\ln[x + 1]$ ) to meet the assumptions of ANOVA (Zar 1984). Root biomass ( $\ln[x + 1]$  transformed) and root : shoot biomass ratio ( $\sqrt{x}$  transformed) of the three morphotypes in the backdune were analyzed following the same procedure. The Scheffé test was used for pairwise comparisons.

We recognize that we did not truly replicate habitat type. However, to have replicates of several sites each of backdune, bluff scrub, and coastal grassland would have been extremely time-consuming; also, all the surrounding lands are owned by the California Department of Parks, and recreation and introduction of cuttings there is prohibited. We are confident that our sites are typical of these three habitats in terms of vegetation cover, species composition, and evidence of animal activity (Albert 1995a). Our design is common for simultaneously comparing the effect of several ecological factors (i.e., herbivory and water availability) among vegetation types. Furthermore, we did not include habitat as a factor in the ANOVAs; rather, we tested our results by a different ANOVA for each habitat and qualitatively compared results among habitats.

## RESULTS

### Growth of naturally occurring plants

There were significant differences among *Carpobrotus* morphotypes in stem length on naturally occurring clones in both backdune ( $F_{1,68} = 35.73$ ,  $P = 0.0001$ ) and bluff scrub habitats ( $F_{2,51} = 17.21$ ,  $P = 0.0001$ ) (Fig. 1). In the backdune, hybrid morphotypes had greater stem length than *C. chilensis* (Scheffé test,  $P < 0.05$ ). In the bluff scrub, *C. edulis* and hybrid morphotypes had higher stem length than *C. chilensis* (Scheffé test,  $P < 0.05$ ). Average stem length of *C. edulis* and hybrid morphotypes was similar (Scheffé

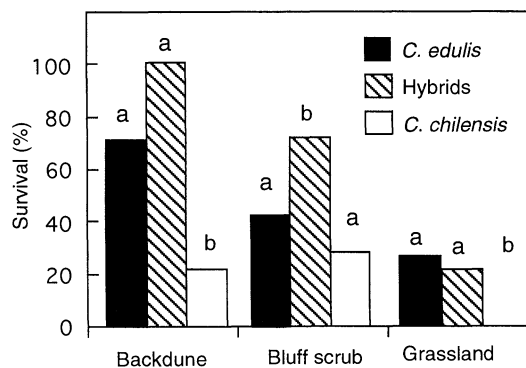


FIG. 2. Percentage survival of uncaged *Carpobrotus* cuttings over one year in a backdune, bluff scrub, and grassland in Bodega Marine Reserve. Significant differences among morphotypes within a habitat are indicated by different lowercase letters.

TABLE 2. Effects of watering and caging on the survivorship of cuttings of three *Carpobrotus* morphotypes transplanted into the three study habitats. Data were analyzed by  $\chi^2$  deviance of the loglinear model.

Source of variation	df	Change in scaled deviance†
Habitat (H)	2	13.40*
Morphotype (M)	2	59.17*
Water (W)	1	2.69
Caging (C)	1	51.92*
H × M	4	9.69*
H × W	2	5.40
H × C	2	12.12*
M × W	2	0.66
M × C	2	10.00*
W × C	1	0.11
H × M × W	4	3.09
H × M × C	4	11.59*
H × W × C	2	2.01
M × W × C	2	2.01
H × M × W × C	4	5.15

\*  $P < 0.05$ .

† For each factor, change in scaled deviance measures the size of the discrepancy between the observed proportion of cuttings that survived and the fitted values produced by the logit function for proportion data with binomial errors.

test,  $P > 0.05$ ). Hybrid and *C. chilensis* stem length showed a strong trend toward a difference among habitats, with hybrids having higher growth ( $F_{1,68} = 3.65$ ,  $P = 0.06$ ).

#### Survival of transplanted cuttings

Only half of the uncaged cuttings survived; survival was significantly different among morphotypes and habitats (Fig. 2). At the backdune, all uncaged hybrid cuttings survived, while 71% of *C. edulis* and only 21% of *C. chilensis* survived. At the bluff scrub, survival of uncaged parental cuttings (*C. edulis* 43% and *C. chilensis* 21%) deviated significantly from the loglinear-generated model, and was lower than that of hybrid morphotypes (71%). Overall, survival was lower in the grassland (17%) than in the other two habitats. There, all uncaged *C. chilensis* cuttings died or disappeared, while 29% of *C. edulis* and 21% of hybrid

morphotypes survived. Cutting survival was not affected in any way by watering (Table 2).

#### Performance of transplanted cuttings

*Effect of watering and caging.*—Growth responses to caging differed among habitats (Tables 3, 4). Caged *C. edulis* and hybrid cuttings always had higher stem length (Fig. 3) and relative growth (Fig. 4) than uncaged plants, except in the bluff scrub, where there was no effect of caging. The effect of caging on *C. chilensis* stem length and relative growth could not be assessed because of the high mortality of uncaged plants.

Despite the above-average rainfall during this study (1671 mm from May 1994 through May 1995), watering increased relative growth of all morphotypes in all habitats (Fig. 4). Watering also increased stem length for all types in all habitats except for *C. edulis* in the grassland (Fig. 3).

Caging had no significant effect on the root biomass of cuttings of *C. edulis* and hybrid morphotypes harvested in the backdune ( $F_{1,72} = 2.12$ ,  $P = 0.15$ ). However, watering increased root biomass of these morphotypes ( $F_{1,72} = 13.91$ ,  $P = 0.0004$ ). Neither herbivory nor watering affected root : shoot ratios of *C. edulis* and hybrid morphotypes ( $F_{1,72} = 2.85$ ,  $P = 0.09$  and  $F_{1,72} = 2.86$ ,  $P = 0.09$ , respectively) (Fig. 5). So few uncaged *C. chilensis* cuttings survived that they could not be statistically analyzed for root biomass.

*Growth differences among morphotypes.*—We found differences in clonal growth between caged parental and hybrid morphotypes (Table 4). Hybrids always had higher relative growth and greater stem length than *C. chilensis*. However, hybrid morphotypes performed better than *C. edulis* only at the backdune (Scheffé test,  $P < 0.05$ ). At the backdune and bluff scrub, caged *C. edulis* relative growth was not significantly different from that of *C. chilensis* cuttings (Scheffé test,  $P > 0.05$ ), but on the grassland, caged *C. edulis* had higher relative growth than *C. chilensis* (Scheffé test,  $P < 0.05$ ) (Fig. 4). Neither stem length nor root biomass were significantly different among parental morpho-

TABLE 3. Analysis of variance for performance (relative increase in stem length and aboveground biomass) of *C. edulis* and hybrid transplanted cuttings at the backdune, bluff scrub, and grassland study sites. Data are sums of squares.

Source of variation	Backdune			Bluff scrub			Coastal grassland		
	df	Relative increase		df	Relative increase		df	Relative increase	
		Stem length	Biomass		Stem length	Biomass		Stem length	Biomass
Block	13	5.32	8.42	13	16.71*	21.82	13	4.89	8.13
Water (W)	1	3.66**	7.77**	1	10.11***	20.75***	1	1.79**	3.27**
Caging (C)	1	3.44**	6.35**	1	1.03	1.45	1	4.46****	13.68***
Morphotype (M)	1	6.25***	7.48***	1	0.53	0.00	1	0.02	0.08
W × C	1	0.37	0.08	1	0.21	0.51	1	0.05	0.04
W × M	1	0.07	1.10	1	0.07	0.12	1	1.30*	1.22
C × M	1	0.28	0.91	1	0.54	0.18	1	0.07	0.01
W × C × M	1	0.02	0.00	1	0.23	0.09	1	0.68	0.56
Residual	76	29.86	42.94	54	30.21	48.46	48	9.78	18.46

\*  $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

TABLE 4. Analysis of variance for performance (relative increase in stem length and aboveground biomass) of *C. edulis*, *C. chilensis* and hybrid transplanted cuttings protected from herbivory at the backdune, bluff scrub, and grassland study sites. Data are sums of squares.

Source of variation	Backdune			Bluff scrub			Coastal grassland		
	df	Relative increase		df	Relative increase		df	Relative increase	
		Stem length	Biomass		Stem length	Biomass		Stem length	Biomass
Block	13	5.11	9.63	13	11.25	22.72	13	2.94	6.76
Water (W)	1	3.32**	5.72***	1	9.60***	20.68***	1	1.24*	2.85**
Morphotype (M)	2	5.03**	8.35***	2	4.11	5.83	2	2.13**	9.50***
W × M	2	0.08	0.64	2	0.03	0.01	2	0.06	0.48
Residual	49	15.86	20.30	38	26.76	39.90	47	9.72	20.24

\*  $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

types (Scheffé test,  $P > 0.05$ ) (Fig. 3). In the absence of herbivory, hybrid morphotypes had more roots than *C. chilensis* (Scheffé test,  $P < 0.05$ ), but similar root biomass to *C. edulis* cuttings.

#### DISCUSSION

##### Hybrid vigor in the wild

Hybrid vigor, defined as superior vegetative growth or reproductive output, greater resistance to diseases, or better tolerance for stress of hybrids compared to parental lineages, has traditionally been quantified for cultivars in agronomy (e.g., Walton 1971, Schonweis and Erickson 1989, Percy and Turcotte 1991); it has been suspected to occur in wild hybrids between previously allopatric species (e.g., Thompson 1991, Abbott 1992). However, few prior studies have related possible hybrid vigor in the wild to successful biological invasions (Williamson 1996). In this study we have demonstrated that hybrid morphotypes exhibited hybrid vigor for several clonal growth characters. Hybrid cuttings were superior in biomass increase compared to *C. chilensis* in the backdune and grassland and superior to *C. edulis* in the backdune. Hybrids never had lower survival or growth than parental species. Our results are contradictory to the ephemeral hybrid zone hypothesis (Dobzansky 1970) and the dynamic equilibrium model (Barton and Hewitt 1985), because we did not find hybrids to have inferior survival and growth to parental species in any of the sites we used. This study is complemented by the analysis of reproductive components and seed dispersal of *Carpobrotus* spp., which demonstrated that hybrids do not have lower seed dispersal (Vilà and D'Antonio 1998a) or lower seedling survival (Vilà and D'Antonio 1998b) than parental species.

For the vegetative growth features that we measured, our data support the observation of Rieseberg (1995) that hybrids do not always display intermediate characters to parental ones. Morphometric analysis of *Carpobrotus* in coastal California showed that putative hybrids had leaf and flower characters (leaf size, leaf shape, leaf serration, leaf and flower color) that were intermediate between putative parents (Albert 1995a).

Gottlieb (1984) distinguishes two types of morphological characters that define plant hybrids. Qualitative characters (e.g., leaf shape, presence vs. absence of spinescence, flower color) are the ones that traditionally have been used to assess for plant hybridization by morphological analysis. By contrast, metric characters are those related to components of size, mass, and yield. These traits appear to be influenced by a larger number of loci than are qualitative characters. Although it is difficult to assess the contribution of both character types to plant evolution (Hilu 1983), it

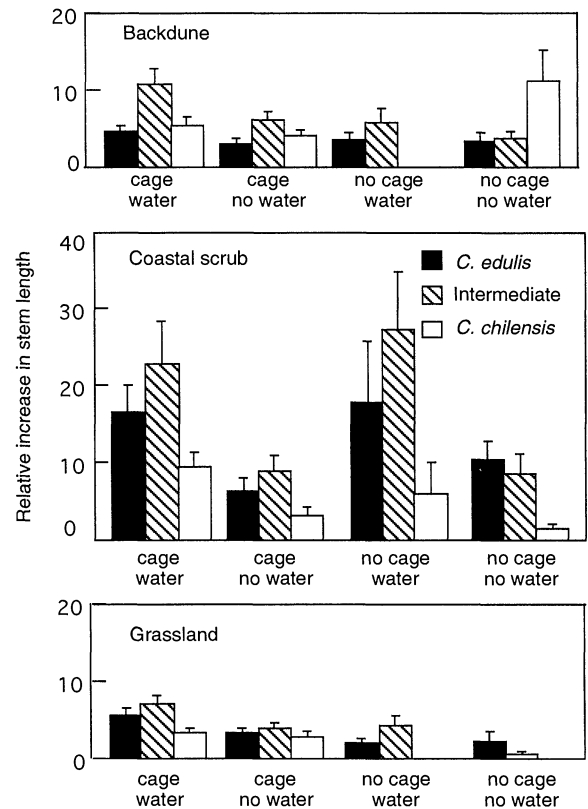


FIG. 3. Relative increase ( $[S_t - S_0]/S_0$ ) in stem length of transplanted *Carpobrotus* cuttings in a backdune, bluff scrub, and grassland in Bodega Marine Reserve. Bars indicate mean + 1 SE.



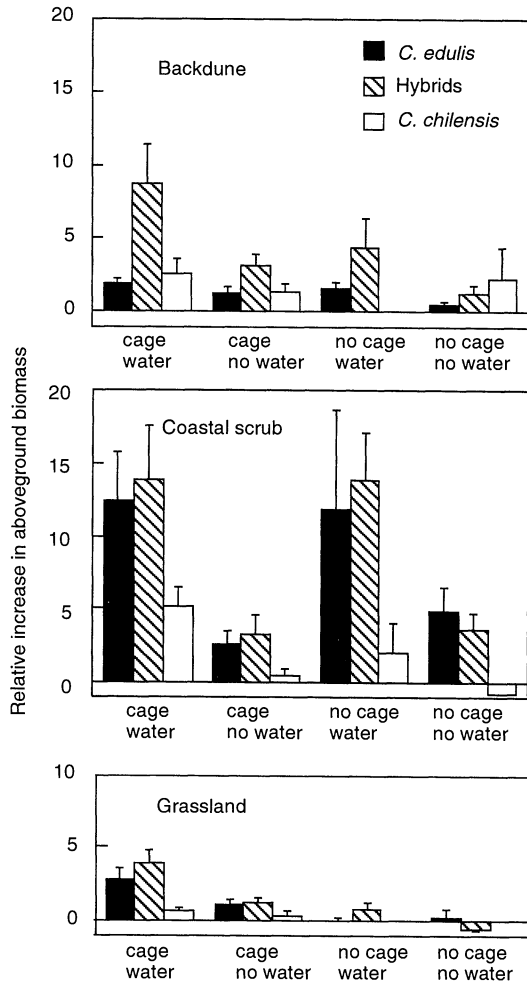


FIG. 4. Relative increase ( $[B_{t_1} - B_{t_0}]/B_{t_0}$ ) in aboveground biomass of transplanted *Carpobrotus* cuttings in a backdune, bluff scrub, and grassland in Bodega Marine Reserve. Bars indicate mean + 1 SE.

is clear that plants that have been classified as intermediates based on taxonomic characters may have higher performance (in this study, growth) than either putative parent. Morphological and molecular descriptions of hybrids coupled with ecological studies are needed to explain the mechanisms that govern hybrid distribution and abundance in the wild, including the paradox of intermediate morphology and superior growth of hybrids.

The underlying mechanisms for hybrid vigor in *Carpobrotus* spp. are unknown. There are strong associations between heterozygosity and measures of plant performance that may be more apparent in certain environments (Mitton and Grant 1984). Using isozyme analyses, Gallagher et al. (1997) show that heterozygosity levels are high in hybrid and introgressed appearing individuals of *C. edulis* from throughout California. Extrinsic factors, i.e., differences in habitat, played an important role in the expression of hybrid

vigor. In the grassland and bluff scrub, the relative growth of putative hybrids was not significantly different from that of *C. edulis*, which had the highest relative growth. In the backdune, by contrast, putative hybrids grew more than either parent species. The most obvious differences among the three habitats studied are plant cover and species diversity. Plots at the backdune were in bare, sandy soils. Cuttings thus experienced little competition but potentially greater water stress. At the other two habitats, vegetative cover was high and soils were more loamy. Transplanted cuttings are likely to have experienced greater competition with established vegetation.

#### Hybrid resistance to herbivory

The importance of plant hybridization in plant-herbivore interactions is attracting increasing attention (Strauss 1994). Relative susceptibility to herbivory of hybrids and parental taxa has been studied mainly with regard to insect herbivory. Such studies have led to contradictory conclusions. In a *Quercus* hybrid complex in northern Sierra Madre Occidental, Boecklen and Spellenberg (1990) found that hybrids supported lower densities of leaf-mining and gall-forming insects than did parental morphotypes, and Graham et al.

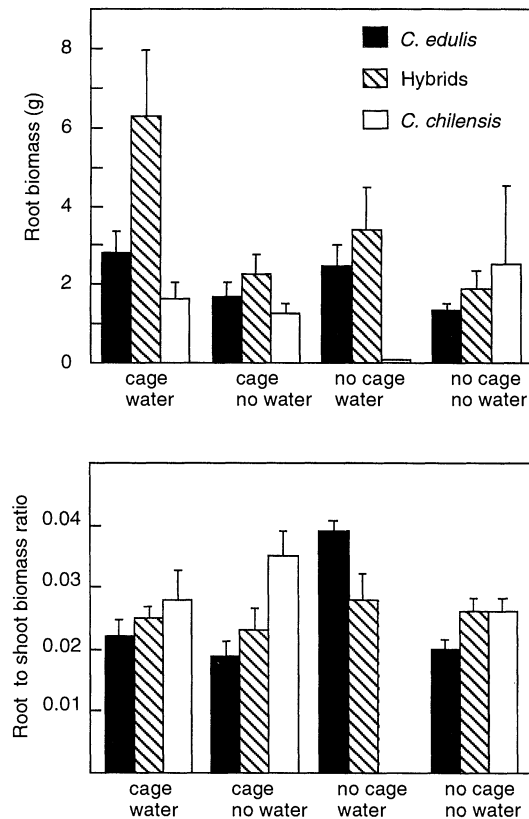


FIG. 5. Root biomass and root:shoot biomass ratio of transplanted *Carpobrotus* cuttings in a backdune in Bodega Marine Reserve. Bars indicate mean + 1 SE.

(1995) found hybrid sagebrush in Utah to be less browsed by grasshoppers than were parent taxa. By contrast, Whitman et al. (1994) found that *Eucalyptus* hybrids in Tasmania had more insects and fungi than did parental species. In our system, generalist mammalian herbivores caused the death of uncaged cuttings. These herbivores were jackrabbits (*Lepus californicus*) and brushrabbits (*Sylvilagus bachmanii* Waterhouse). They do not indiscriminately consume all plant species (Westoby 1974). Rather, they respond to genetic variation in plant defense mechanisms (Pollard 1992). Herbivory had a higher negative effect on *C. chilensis*, the taxon that grew the least. Hybrids often had higher growth rates than did parents, and this higher growth rate may have helped them to overcome damage from herbivore attack. However, we do not know whether the higher survival of *C. edulis* and hybrids was the result of greater resistance to or tolerance to herbivory (Rosenthal and Kotanen 1994).

In our study, hybrid resistance to herbivory was habitat dependent. Survival of putative hybrids was lower in the grassland than in the other two habitats. Survival was similar to *C. edulis* in the grassland and backdune but higher than both parental taxa in the bluff scrub. This suggests that both genetics and environment may affect the outcome of herbivory (Strauss 1990).

#### *Invasive potential of Carpobrotus hybrids in coastal California*

Our findings constitute a warning to managers and policy makers that hybrids have high growth potential, particularly in backdunes and bluff scrub sites. Quantitative observations throughout coastal California demonstrate that *C. edulis* and hybrid clones have fewer native plant species in association with them than do *C. chilensis* clones (Albert 1995a). The higher clonal cover of invasive hybrids compared to *C. chilensis* is related to both higher vegetative growth and greater resistance to mammalian herbivory. Furthermore, *C. chilensis* is rare in coastal grassland throughout California (Albert 1995a), and our data support the hypothesis that this may be due at least in part to intense herbivory.

Our results also have implications for the management of *Carpobrotus* in coastal California. Management control of invasive *Carpobrotus* is performed by spraying clones with Round-up and mechanically pulling clones by the "carpet rolling" technique (Albert 1995b). Our results show that natural processes may help to reduce the growth of *C. edulis* and hybrids. Survival and growth were lowest in the grassland where they were reduced by herbivory, by water limitation, and partially by competition with the existing dense vegetation. D'Antonio (1993) found that soil disturbance (i.e., gopher mounds) was required for *C. edulis* establishment in grasslands because it reduced seedling competition between *C.*

*edulis* and grasses. In our grassland site, cuttings were planted into undisturbed grassland, and growth and survival were poor for all morphotypes. Unquantified observations at Bodega Marine Reserve suggest that rodent and other soil disturbances are indeed the microsites in which *Carpobrotus* establishment occurs within the grassland. Thus, population control of invasive morphotypes will be more effective in grassland communities, where soil disturbance is uncommon but where herbivory is common. In sites such as bluff scrub and backdune communities where there are naturally large patches of bare soil, *Carpobrotus* can establish and grow rapidly.

In conclusion, our study suggests that the overall potential for *Carpobrotus* to occupy California coastal plant communities may be increased by hybridization. Clonal growth is a major factor in the competitive ability of *Carpobrotus*. *Carpobrotus* hybrids should be explicitly listed as exotic pest plants of greatest ecological concern in California because their clonal growth can be even larger and resistance to herbivory higher than those attributes for *C. edulis*.

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