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FRUIT CHOICE AND SEED DISPERSAL OF INVASIVE VS. NONINVASIVE *CARPOBROTUS* (AIZOACEAE) IN COASTAL CALIFORNIA

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Abstract. Natural hybridization between previously allopatric plant species can produce highly successful lineages. However, the ecological processes controlling the spread of hybrid genotypes have rarely been studied in the field. We compared fruit characteristics, fruit preference, and seed dispersal by native frugivores among the non-indigenous succulent *Carpobrotus edulis,* the putative native congener *C. chilensis,* and the hybrids resulting from introgressive hybridization. In this system, the non-native *C. edulis* and hybrids are known to be very successful invaders of California coastal plant communities. *Carpobrotus edulis* and hybrids produced more fruits per clone than *C. chilensis,* primarily as a consequence of larger clone size. Clone size and energy content of fruits were good predictors of fruit removal. Marked fruits of *C. edulis* and hybrids were removed faster than those of the other morphotypes, and *C. edulis* fruits were preferred over those of *C. chilensis* in a fruit transplant experiment. However, total fruit removal by the end of the growing season was very high for all morphotypes. Scats from black-tailed jackrabbit (*Lepus californicus*) and mule deer (*Odocoileus hemionus*), the most common frugivores in our sites, contained more seeds from *C. edulis* and hybrid morphotypes than from *C. chilensis,* and more than would be expected based on relative fruit abundance. Germination of seeds from *C. edulis* and hybrids was enhanced after gut passage, whereas germination of *C. chilensis* decreased after gut passage, compared to seed germination from intact fruits. The results suggest that patterns of fruit preference by native frugivores and seed survival after gut passage facilitate the successful spread of an aggressive introduced species and hybrids in contrast to the less aggressive, apparently native congener.

Key words: Aizoaceae; Carpobrotus chilensis; Carpobrotus edulis; fleshy fruit; fruit preference; fruit quality; gut passage; hybridization; mammal frugivory; nonindigenous species; plant invasion; seed dispersal.

INTRODUCTION

One consequence of species introduction may be the appearance and persistence of hybrid morphotypes (Abbott 1992). Hybridization between native and non-native plants may result in invasive hybrid morphotypes that, in turn, have dramatic effects on the communities in which they occur (Thompson 1991, Rieseberg and Wendel 1993). For example, both non-native and hybrid introduced fleshy fruited plant species may compete for dispersal agents with previously established species, particularly congeners with similar fruiting displays (Gade 1976).

Previous studies attempting to elucidate the fitness of hybrid individuals (reviewed by Arnold and Hodges 1995) have not included fruit choice and seed dispersal stages in the reproductive analysis, although these steps are critical to understanding the potential for spread of hybrids. Foraging behavior studies have shown that vertebrate frugivores do not consume fruit at random

with respect to fruit and crop characteristics. For bird-dispersed species in north-temperate regions, fruit characteristics such as morphology, size, seediness, and content of edible tissues (Herrera 1981, Debussche and Isenmann 1989), nutritional content (Sorensen 1981, Herrera 1992), phenology, and timing of fruit maturation (Stiles 1980, Sorensen 1981), and crop size and local fruit abundance (Murray 1987, Sargent 1990) have been shown to influence fruit preference. For fleshy fruited plants, an investigation of the role of frugivores in seed dispersal of hybrid and putative parental genotypes may help us to understand why some closely related taxa are more attractive to frugivores and, therefore, might spread more rapidly than their congeners. Thus, the importance of frugivory to the success of introduced species and hybrids should be compared to that of closely related, previously established taxa (Debussche and Isenmann 1990, Sallabanks 1993*a*).

Hybridization between the non-native succulent *Carpobrotus edulis* L. Bolus and the previously established *C. chilensis* L. is occurring in coastal California (Albert et al. 1997, Gallagher et al. 1997). *Carpobrotus edulis* is invading coastal communities and is an aggressive competitor against native species (D'Antonio and Ma-

hall 1991). Hybrids are abundant and appear to exclude native species (Albert 1995). In spite of this, little is known about the fitness and potential for spread of hybrids, or how dispersal and establishment compare among *C. edulis, C. chilensis,* and hybrids. In this study, we address the following questions. (1) Are there differences in fruit production, phenology, and fruit quality (size, proportion of edible tissues, and nutritional content) among *Carpobrotus* morphotypes? (2) Are fruits of the invasive morphotypes consumed more than those of the non-invasive morphotypes? (3) Does fruit preference result in higher seed dispersal of the preferred morphotypes? Based on the large number of *C. edulis* and hybrid morphotypes in coastal California, we hypothesized that *C. edulis* and hybrids have fruits that are more appealing, and their seeds are more dispersed than those of *C. chilensis.*

METHODS

Study species and site

Carpobrotus spp. (Aizoaceae) are perennial succulents easily recognized by their trailing habit and succulent, three-angled leaves (Wisura and Glen 1993). In coastal California, two species of *Carpobrotus* occur, both producing indehiscent, fleshy fruits that are consumed by native mammals. *Carpobrotus edulis* was introduced from South Africa to the Pacific coast of North America in the last century for dune stabilization, and has now been extensively planted along roadsides. It has invaded natural coastal communities in California through the dispersal of its seeds by native mammals (D'Antonio 1990) and through high clonal growth rates after establishment (D'Antonio 1993). It is an aggressive competitor against native species (D'Antonio and Mahall 1991). By contrast, *C. chilensis* is a noninvasive species that co-occurs in most of the same habitats as *C. edulis.* It grows as sparse patches of long, thin branches intermingled with the established vegetation. The native status of *C. chilensis* is not clear. It does not occur in South Africa (Wisura and Glen 1993), but appears to be unique to California (N. Vivrette, *personal communication*), where it has occurred since at least the 1600s (Bicknell and Mackey 1988).

According to leaf and flower characteristics, intermediate morphotypes between the two species are present in several habitats along the Californian coast (Albert et al. 1997). Analysis of isozyme markers supports the conclusion that introgressive hybridization is taking place and that introgression is occurring primarily in the direction of *C. edulis* (Gallagher et al. 1997). Putative hybrids and introgressants resemble *C. edulis* in their matlike and aggressive growth habits (M. Vilà and C. M. D'Antonio, *unpublished data*). For the purpose of this study, we compared three taxa: the two parental species and intermediate morphotypes ("hybrids" hereafter).

Observations and experiments were carried out in

1994 and 1995 in Bodega Bay Marine Reserve in northern California (38°19′, 123°4′), where both putative parental populations and hybrid morphotypes co-occur (Albert et al. 1997, Gallagher et al. 1997). The site is a coastal bluff scrub dominated by the shrubs *Eriophyllum staechadifolium* Lag. var. *artemisiaefolium* Lagasca and *Erigeron glaucus* Ker-Gawler, and the grasses *Bromus carinatus* Hook & Arn. and *B. diandrus* L.

Fruiting phenology and fruiting-crop patterns

We compared the number of fruits present and number of fruits removed (i.e., eaten) for each of the three morphotypes in one permanent quadrat (0.25 m²) within each of 20 clones of *C. chilensis* and hybrids and 15 clones of *C. edulis,* during the first week of each month from April 1994 to March 1995. The effects of morphotype on the numbers of fruits present and removed in October 1994 were compared by log-linear analysis (Zar 1984). The relationship between clone area and total numbers of fruits present and removed per clone was examined by regression analysis.

Fruit characteristics

Structural fruit characteristics were compared among morphotypes as follows: we collected three fruits from 12 clones of each morphotype and counted the number of seeds in one loculus per fruit. The total number of seeds per fruit was then estimated by multiplying the number of seeds in that loculus by the number of loculi per fruit. Previously, we had determined that loculi within a fruit contained the same number of seeds, based on counting the number of seeds in four loculi per fruit in 12 fruits of each morphotype. The number of seeds per loculus did not vary significantly within a fruit morphotype (one-way nested ANOVA $F_{3, 138} = 0.066$, $P = 0.98$). Dry mass of fruits was also measured after drying these fruits at 60°C until constant mass was attained. Two fruits from each of 13 clones of *C. edulis* and hybrids, and 15 clones of *C. chilensis* were weighed and dissected into coat, pulp, and seeds. All fruit portions were then dried at 60°C to constant mass. The net dry pulp and coat (pericarp), pericarp : seed biomass ratio, and water content of the fruit were compared among morphotypes after averaging the two values from each clone.

Total protein content of the pericarps was estimated for two fruits in six clones of each parental species and eight clones of hybrids. Total N content was measured by elemental analysis, and total protein content was calculated by multiplying the percentage of N by 6.25 (Herrera 1992). Soluble carbohydrate content was determined after boiling the fruit sample in distilled water and using the colorimetric method described by Allen (1974). The relative energy content of fruits was calculated by multiplying the mass of proteins and the mass of carbohydrates (both measured in grams) by 4.

The effect of morphotype on fruit characteristics was

analyzed by a one-way ANOVA. Data were log- or square-root transformed, when necessary, to obtain homogeneity of variances and normality of errors.

Fruit removal rates and fruit choice

The removal rate of fruits in the coastal shrubland was determined by using metallic tags to randomly label five ripe fruits in an area of 1 m² within each of 10 clones per morphotype in October 1994. The number of fruits that had disappeared was tallied at irregular intervals over the next 70 d. We are confident that labeling with a metallic tag did not attract frugivores, because labels did not get chewed and rates of fruit removal of marked fruits matched those of unmarked fruits at the study site. Numbers of fruits remaining at each sampling date were pooled for each morphotype, and fruit removal curves were compared by the Gehan-Wilcoxon test (Pyke and Thompson 1986) and by pairwise comparisons of curves, using the Kolmogorov-Smirnov test (Zar 1984). The proportion of removed fruits at the end of the survey was compared among morphotypes, using a chi-square test.

To assess fruit choice among morphotypes and among fruits belonging to different morphotypes, we conducted a fruit transplant experiment, in which fruits were relocated into the same or different morphotypes. Mature fruits were removed from 10 clones per morphotype, and two fruits of each morphotype were placed into a haphazardly selected area of ~2 m² within each clone. This density (3 fruits/m²) matched natural fruit density during that month (October 1994). Transplanted fruits were individually pinned with wooden toothpicks to reproductive stems where fruits had been located. Seven days later, the remaining transplanted fruits were counted. Fruit removal was analyzed using a log-linear approach, with clone and fruit morphotype as main effects.

Seed dispersal

To compare actual dispersal of *Carpobrotus* morphotypes, fresh droppings of black-tailed jackrabbit (*Lepus californicus* Gray) and mule deer (*Odocoileus hemionus* Colombianus) were haphazardly collected in October 1995 and examined for seeds. The number of intact seeds of each morphotype was recorded for 25 fresh piles of up to six droppings from each frugivore. Seeds were examined under a magnifying lens (40×) and were compared with the morphology of intact seeds from uneaten ripe fruits. Seeds of the three types are distinguishable from each other: *C. edulis* oval seeds have a smooth coat, with the hilum at terminal position, whereas *C. chilensis* seeds are wrinkled, with the hilum at lateral position. Hybrid seeds are more circular than those of *C. edulis,* and have a smooth coat with the hilum at lateral position.

We used a chi-square test to compare the observed number of seeds in scat for each frugivore with an expected number of seeds from each morphotype. We assumed that foraging patterns for both jackrabbits and deer were evenly distributed in the study site, because of its small size (~15 ha) and microgeographic homogeneity. The expected number of seeds was calculated as:

$$\text{Expected} = S \times F \times A$$

where S is the estimated number of seeds per fruit; F is the number of fruits per *Carpobrotus* unit area at the beginning of October 1995, according to the phenology survey; and A is the percentage of ground cover at the site occupied by the particular *Carpobrotus* morphotype.

To compare the effect of gut passage on seed viability, we tested nine replicates of 10 seeds from each morphotype for germinability by sowing them on moist, washed sand in covered petri dishes at 20°C on a 9:11 daylight cycle. Germination was compared to that of nine replicates of 10 seeds randomly selected from a pool of 10 ripe, intact fruits from each morphotype. Fifty days after initiating the germination tests, we tested the viability of intact seeds that had not germinated by staining them with 0.1% tetrazolium after piercing and soaking them in 400 mg/L gibberellic acid at 4°C overnight (Ellis et al. 1985).

We used a two-way ANOVA to determine the effect of seed morphotype and its origin (intact ripe fruit, jackrabbit or deer scat) on the proportion of germinated seeds at the end of the test. The effect of morphotype and frugivore on viability of the seeds that had not germinated was tested by an extension of the Kruskal-Wallis test (Zar 1984).

RESULTS

Fruiting phenology and fruiting-crop patterns

The mean number of fruits increased continuously from April to July for all morphotypes, and began to decrease in September. Seven out of 20 hybrids did not set flowers or produce fruits, whereas all *Carpobrotus edulis* and *C. chilensis* clones produced fruits. *Carpobrotus edulis* and hybrids had no fruit left after October, but at least a few fruits of *C. chilensis* persisted until January. In *C. edulis* and hybrids, fruit consumption started in August and ended in November; in *C. chilensis,* it started one month earlier.

Clone size differed significantly among morphotypes ($F_{2,54} = 42.84$, $P = 0.0001$). Hybrids occupied large mats (75.72 ± 27.87 m², mean ± 1 SE) that were approximately two times bigger than those of *C. edulis* (36.03 ± 9.90 m²). *Carpobrotus chilensis* clones were the smallest: individual clones occupied 1.93 ± 0.49 m². In our study site, hybrids occupied the largest ground area (27% of total ground cover), whereas *C. edulis* and *C. chilensis* occupied 2.42% and 8.42%, respectively.

There were significant differences in the number of fruits per clone in October 1994 ($\chi^2 = 9938.16$, df =

TABLE 1. Characteristics of ripe *Carpobrotus* fruit morphotypes at Bodega Marine Reserve. Values are mean ± 1 SE, with number of fruits sampled reported in parentheses.

Characteristic	C. edulis	Hybrids	C. chilensis	
Dry mass (g)	$4.09^a \pm 0.14$ (36)	$1.68^b \pm 0.11$ (36)	$0.71^c \pm 0.50$ (36)	$F_{2,103} = 0.15^{***}$
No. seeds/fruit	$1573^a \pm 65$ (36)	$704^b \pm 43$ (36)	$483^b \pm 27$ (36)	$F_{2,103} = 83.70^{***}$
Pericarp mass (g)	$2.25^a \pm 0.09$ (13)	$0.92^b \pm 0.13$ (15)	$0.25^c \pm 0.02$ (13)	$F_{2,38} = 0.01^{***}$
Pericarp:seed mass ratio	$3.18^a \pm 0.36$ (13)	$10.12^b \pm 2.45$ (13)	$6.39^{a,b} \pm 1.69$ (15)	$F_{2,38} = 8.36^{***}$
Water content (%)	$80.56^a \pm 0.57$ (14)	$78.17^a \pm 0.94$ (13)	$80.54^a \pm 0.59$ (16)	$F_{2,38} = 3.68^*$
Protein content (g/g)	$0.12^a \pm 0.02$ (6)	$0.34^a \pm 0.12$ (8)	$0.17^a \pm 0.02$ (6)	$F_{2,17} = 3.45$NS
Soluble carbohydrate content (g/g)	$0.68^a \pm 0.14$ (6)	$2.10^b \pm 0.69$ (8)	$0.75^{a,b} \pm 0.12$ (6)	$F_{2,17} = 5.37^*$
Energy content (kJ/fruit)	$8.53^a \pm 0.75$ (6)	$3.72^b \pm 0.50$ (8)	$1.17^c \pm 0.17$ (6)	$F_{2,17} = 55.85^{***}$

Note: Protein and soluble carbohydrate content values are grams of nutrients per gram dry mass of the whole fruit.
* $P < 0.05$; ***$P < 0.001$; NS, nonsignificant. Values with different superscripts within a row are statistically different (Scheffé test, $P < 0.05$).

2, $P > 0.0001$). *Carpobrotus edulis* and hybrids bore, on average, 497 and 366 fruits per clone, whereas *C. chilensis* had only 13 fruits per clone. The number of fruits was significantly correlated with clone area ($r^2 = 0.69$ for *C. edulis*; $r^2 = 0.69$ for hybrids; $r^2 = 0.62$ for *C. chilensis*; $P = 0.0001$). The number of fruits removed per clone was also significantly different among morphotypes ($\chi^2 = 8655.9$, df $= 2, P > 0.0001$), and it was also correlated with clone area. Clone area accounted for 69%, 48%, and 23% of the variation in the number of fruits removed from *C. edulis,* hybrids, and *C. chilensis,* respectively.

Fruit characteristics

Carpobrotus produces fig-like, fleshy fruits with ~80% water content when ripe. *Carpobrotus edulis* fruits were significantly larger than the two other morphotypes, and hybrid fruits were intermediate between the two species (Table 1). This difference in fruit size
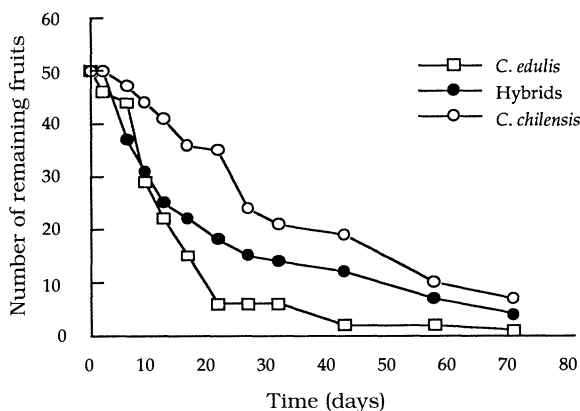

FIG. 1. Removal curves for tagged fruits of *Carpobrotus* at a coastal shrubland in Bodega Marine Reserve in the fall of 1994; $N = 50$ fruits per species and hybrids.

was due to differences in both the pericarp biomass and the number of seeds per fruit. *Carpobrotus edulis* had approximately three times more seeds per fruit than the other two morphotypes. Overall, fruit quality, in terms of digestible biomass (pulp plus coat) vs. nondigestible biomass (seeds), was higher in hybrids than in *C. edulis.* The pericarp: seed biomass ratio of *C. chilensis* was not significantly different from that of the other two morphotypes. There were no significant differences in fruit protein content among morphotypes. Hybrid fruits had higher soluble carbohybrates than *C. edulis* and did not differ from *C. chilensis.* The energy content of hybrid fruits fell between the values of parental species (Table 1).

Fruit removal rates and fruit choice

The temporal pattern of fruit removal was significantly different among the three morphotypes ($\chi^2 = 26.103$, df $= 2, P = 0.0001$; Gehan-Wilcoxon test). However, >90% of the tagged fruits were consumed within 2 mo after marking them, and there were no significant differences in the proportion of fruits removed after 70 d ($\chi^2 = 0.391$, df $= 2, P = 0.822$; Fig. 1). Fruits of *C. chilensis* were removed more slowly than fruits of *C. edulis* and hybrids (Kolmogorov-Smirnov test, $D = 0.58, P = 0.001$ and $D = 0.34, P = 0.006$, respectively). Removal rates for *C. edulis* and hybrids did not differ (Kolmogorov-Smirnov test, $D = 0.24, P = 0.112$).

The transplant experiment showed that fruits of the three morphotypes were not equally preferred ($\chi^2 = 8.14$, df $= 2, P = 0.017$; Fig. 2). Fruits of *C. edulis* were preferred (98.33%) over *C. chilensis* fruits (53.33%). The 75% removal of hybrid fruits was not significantly different from that of either parental species. The morphotype into which fruits were trans-
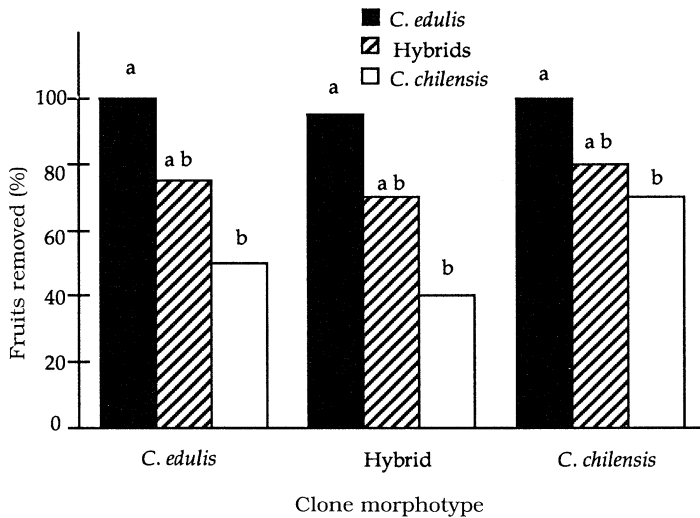
FIG. 2. Percentages of transplanted fruits removed from clones at the three *Carpobrotus* morphotypes by frugivores 7 d after fruits were transplanted at a coastal shrubland in Bodega Marine Reserve. Bars with different letters show significant differences within a clone morphotype.
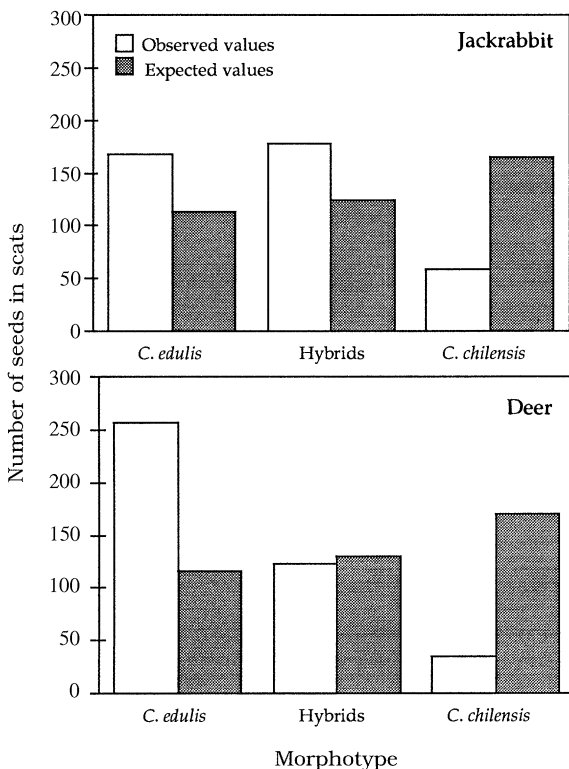

FIG. 3. Number of *Carpobrotus* seeds in jackrabbit and deer scats at a coastal shrubland in Bodega Marine Reserve. Observed values were the number of intact seeds recorded for 25 haphazardly collected fresh scats from each frugivore. Expected values were obtained by estimating the number of seeds per fruit × number of fruits per unit of clone area × percentage of ground cover of a morphotype in the study site.

planted had no significant effect on the patterns of fruit removal ($\chi^2 = 0.993$, df $= 2$, $P = 0.911$).

Seed dispersal

Of the fresh jackrabbit and deer droppings, 29% contained all three seed morphotypes. However, the proportion of seeds of *C. chilensis* was consistently lower than that of *C. edulis* and hybrids. In both types of scats, the proportion of observed seeds did not match the proportion expected based on their abundance in the environment ($\chi^2 = 117.66$, df $= 2$, $P = 0.0001$; and $\chi^2 = 282.27$, df $= 2$, $P = 0.0001$ for jackrabbit and deer, respectively). The observed number of seeds was lower than expected for *C. chilensis* and higher than expected for *C. edulis* and hybrids, in both jackrabbit and deer scats (Fig. 3).

Seeds from the three morphotypes had different germination success under the conditions tested ($F_{2,67} = 35.38$, $P = 0.001$; Fig. 4). More than 74% of *C. chilensis* seeds from intact fruits germinated; this value was higher than for hybrids (13%) or *C. edulis* (4%). In seeds from scat, germination of *C. chilensis* dropped to 31%, whereas germination of hybrid and *C. edulis* seeds was enhanced relative to uneaten seeds (43% and 16%, respectively). In both types of scats, seeds from hybrids had the highest germination success (Scheffé test, $P = 0.001$ when compared with *C. edulis*, and $P = 0.037$ when compared with *C. chilensis*; Fig. 4). Less than half of the ungerminated seeds were viable for all morphotypes, and there were no significant differences in percentage viability of nongerminated seeds among morphotypes (Kruskal-Wallis test, $H = 0.803$, $P = 0.455$).

DISCUSSION

Carpobrotus spp. fruit removal was very high (>90%) for all morphotypes. Fruits of nonindigenous invasive *C. edulis* and hybrids were more preferred and
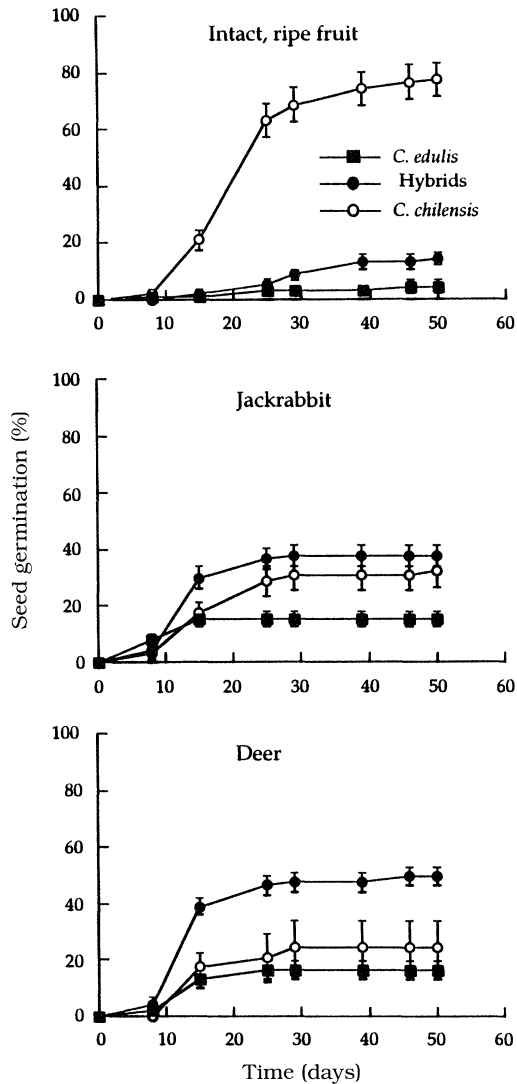
FIG. 4. Germination curves of *Carpobrotus* seeds from intact ripe fruits vs. from jackrabbit and deer scats found at a coastal shrubland in Bodega Marine Reserve. Values represent the mean percentage (± 1 SE) of total seeds that had germinated.

were removed faster than fruits of the noninvasive *C. chilensis*. Seeds of *C. edulis* and hybrids were dispersed more than seeds of *C. chilensis,* and seed germination was enhanced after gut passage.

We found significant differences in *Carpobrotus* fruit characteristics among morphotypes: e.g., an animal must eat two hybrid and seven *C. chilensis* fruits to get the same energy reward provided by one *C. edulis* fruit. Moreover, as a result of differences in fruit production, *C. edulis* and hybrids provide 4235.84 and 111.42 kJ per clone, respectively, whereas *C. chilensis* provides only 15.02 kJ per clone. Fruit preference has been shown to depend on more than one criterion (Howe and Smallwood 1982, Herrera 1989, Hedge et

al. 1991, Jordano 1992), and frugivores can detect very subtle differences between fruits (Levey and Grajal 1991). As proposed by Sallabanks (1993*b*), a species with a high-density per plant fruit display can achieve greater removal success because: (1) fruits are conspicuous and more likely to be seen (Howe and Estabrook 1977, Sallabanks 1992); and (2) once the plant has been found, frugivores obtain a high reward quickly (Martin 1985). We suggest that the large fruit crop of all *C. edulis* and some hybrids, plus the high individual fruit size and energy value, may increase the benefit/cost ratio of handling these fruits. However, fruit choice experiments with captive frugivores would be needed to conclude which *Carpobrotus* fruit characteristics are responsible for fruit preference (Levey and Grajal 1991).

Dispersal prior to the onset of fall rains may allow seeds to germinate when the weather is most favorable. Because frugivory is the only obvious means of seed dispersal for *Carpobrotus,* and unconsumed fruits dry out in the plant, timing differences of fruit choice may have important effects on seed dispersal in these plants.

Some individual scats from black-tailed jackrabbit and mule deer contained all types of *Carpobrotus* seeds, indicating that (1) seeds of all morphotypes are dispersed by the same frugivores, and (2) a single animal forages in all morphotypes in a relatively short period of time. Generally, small seeds (<3 mm) within fleshy fruits consumed by mammals escape mastication and are swallowed without harm (van der Pijl 1972, Janzen 1979, D'Antonio 1990). However, we found broken seeds of unknown morphotype in scats. In addition, even though the overall *C. chilensis* seed set in our study site was higher than for the other morphotypes (Fig. 3), scats contained less *C. chilensis* seeds than expected. There are two plausible reasons for this: first, seeds of *C. chilensis* may be less represented in scats due to lower preference for these fruits. Second, the reduction of seed germination after gut passage, compared to no gut passage for *C. chilensis,* suggests that *C. chilensis* seeds may be more negatively affected by gut enzymes or mastication than those of the other morphotypes. In *C. chilensis,* seeds are smaller, with a softer seed coat than in the other morphotypes (M. Vilà, *personal observation*), and may be more easily damaged.

Carpobrotus hybrid fitness, measured by seed dispersal, was as good as that of *C. edulis* and better than that of *C. chilensis.* Even if some hybrid clones did not flower and variation in fruit crop size was high, we found that most invasive morphotypes had large fruit crops, large, energy-rich fruits, and small seeds with hard coats that remain viable after gut passage. Although the fate of dispersed seeds and seedlings depends on postdispersal factors that may be independent of maternal effects or the number of seeds dispersed (D'Antonio 1993, Herrera et al. 1994, Jordano and Herrera 1995), an increase in seed dispersal should increase fitness. The higher dispersal of *C. edulis* and hybrid

morphotypes may increase the seed bank of these types relative to *C. chilensis*. This seed bank and dispersal away from the parent plant may be essential for colonization after disturbance (e.g., D'Antonio et al. 1993) and for the successful spread of *Carpobrotus* hybrids in coastal California. Hybrids have higher vegetative growth and are less attacked by mammal herbivores than are parental species in certain habitats (M. Vilà and C. M. D'Antonio, *unpublished data*). Thus, because fruit production and removal are dependent on clone size, hybrid fruits will generally be as appealing, and their seeds as well dispersed, as those of *C. edulis* and more so than those of *C. chilensis*.

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