patterns suggest that the persistence of Pangaea throughout the Triassic provided few barriers for the migration of terrestrial vertebrates. The initial stages of rifting in the Late Triassic resulted in no corresponding provinciality of terrestrial vertebrate distribution by the Early Jurassic.

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Salicornia bigelovii Torr.: An Oilseed Halophyte for Seawater Irrigation

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The terrestrial halophyte, *Salicornia bigelovii* Torr., was evaluated as an oilseed crop for direct seawater irrigation during 6 years of field trials in an extreme coastal desert environment. Yields of seed and biomass equaled or exceeded freshwater oilseed crops such as soybean and sunflower. The seed contained 26 to 33 percent oil, 31 percent protein, and was low in fiber and ash (5 to 7 percent). The oil and meal were extracted by normal milling equipment, and the oil was high in linoleic acid (73 to 75 percent) and could replace soybean oil in chicken diets. The meal had antigrowth factors, attributed to saponins, but could replace soybean meal in chicken diets amended with the saponin antagonist, cholesterol. *Salicornia bigelovii* appears to be a potentially valuable new oilseed crop for subtropical coastal deserts.

THERE ARE TWO APPROACHES TO DEveloping crops tolerant of seawater-concentration salinity. One is to increase the tolerance of present crops (*1*), but the difference between the upper limit of salt tolerance currently exhibited by crop plants and that required to tolerate seawater salinity is great (*2*). An alternative is to select from the large pool of halophytes, plants which already have the requisite salt tolerance, those that might make desirable crops (*3*).

Salicornia bigelovii Torr. is a leafless, annual salt-marsh plant with green, jointed, succulent stems that ultimately form terminal fruiting spikes in which seeds are borne (*4*). In subtropical regions it may grow to be a large, upright plant, 50 cm tall, with most of the seed spikes on the upper one-third of the plant. The seeds are approximately 1 mg and germinate directly on seawater. *Salicornia bigelovii* emerged as a potential seawater oilseed crop from a screening of wild halophytes (*5–7*) and was selected for seawater field trials including determination of seed yield and seed analyses.

The trials were conducted at Puerto Peñasco, Sonora, Mexico, in an extreme coastal desert environment at the northern Gulf of California. Seeds were collected near Puerto Peñasco in Estero Morua. Trials in 1982 were conducted in the same 1-ha field and with the same methods previously described for other halophytes (*6*). Trials from 1984 to 1988 were conducted in a 0.5-ha field nearby. Both fields had sandy soils typical of light agricultural soils in the region and were divided into individually irrigated, 200 m^2 flood plots. At both sites irrigation water with a salinity range of 38 to 42 per mil was supplied daily from seawater wells. In field 1, seawater that passed through a shrimp aquaculture facility, which added nitrogen and other nutrients to the water, was used, and no supplemental fertilizer was needed. Field 2 was irrigated with unenriched seawater, and plots received fertilizer additions equivalent to 200 kg of N per hectare or more, as urea, diammonium phosphate, or ammonium nitrate. Rainfall was less than 90 mm annually and the soil in the root zone was at seawater salinity or higher at all times (*6*).

The standard seeding rate of 25 kg ha^{-1} produced a mean plant density at harvest of 323 plants/m^2 (SD, 249; $n = 49$; observa-

Table 1. Summary of annual *Salicornia bigelovii* seed and biomass yields at field 2, Puerto Peñasco, Sonora, Mexico (n, number of plots). Crops were sown during a 2- to 3-week period during the months indicated and were harvested the following September or October in the year indicated. In 1986 12 plots were planted in February and 12 in April.

Month sown	Year	Biomass (kg m^{-2})	SE	n	Seed (g m^{-2})	SE	n
December	1984	2.46	0.18	9	233	13	9
April	1985	1.39	0.04	15	208	11	15
	1986	1.27	0.05	12	177	5	12
February	1986	1.51	0.08	12	193	10	12
	1987	1.98	0.04	15	246	7	15
	1988	1.44	0.09	20	139	11	20

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Table 2. Properties of *Salicornia bigelovii* seed and oil (*18*). Values are means of five or more separate determinations (range of values in parentheses). Amounts are the percentage of total fats for fatty acids and the percentage of seed weights for other constituents.

Constituent	Amount
Oil	28.2 (26–33)
Protein	31.2 (30–33)
Fiber	5.3 (5–7)
Ash	5.5 (5–7)
Fatty acids	
Palmitic	8.1 (7.7–8.7)
Stearic	2.2 (1.6–2.4)
Oleic	12.5 (12.0–13.3)
Linoleic	74.0 (73.0–75.2)
Linolenic	2.6 (2.4–2.7)

tions at field 2). Biomass and seed yields were determined by harvesting all plant material inside three 1-m^2 quadrats per plot. Plants were harvested when the majority of spikes had turned from green to yellow but were still succulent, and they were dried in windrows on the ground. Seed was separated from the dried biomass with a hammer mill to knock the seeds from the spikes and a seed cleaner to separate them (*8*).

At Puerto Peñasco, *S. bigelovii* flowered in mid-June and was ripe in September or October regardless of the sowing date. Thus, crops sown in fall were ready for harvest at approximately the same time as crops seeded in winter or spring. Experiments to determine the effect of planting date on biomass yield (Fig. 1A), seed yield (Fig. 1B), and the ratio of seed to biomass (Fig. 1C) were conducted in 1982 at field 1 and in 1984 in field 2. The regression of biomass on planting date was not statistically significant, but seed yield and percentage of seed increased significantly with advancing planting date up to early April. Between-year differences in slopes of regression equations or means were not statistically significant.

The 1982 mean seed yield at field 1 was 208 g m^{-2} (SE, 9). The variability in biomass and seed yield was investigated by growing multiple plots of *S. bigelovii* for 5 years in field 2 (Table 1). The 1984 plots were sown in December whereas all other plots were sown in February or April. Analysis of variance revealed differences in yield among years at common seeding dates ($P = 0.035$ for April-class seed yields, $P < 0.01$ for February-class seed and biomass yields, and not significant for April-class biomass yields). Annual mean yields at field 2 ranged from 139 to 246 g m^{-2} with a 5-year mean of 199 g m^{-2}. Thus, during 6 years at two fields, *S. bigelovii* seed yields equaled or exceeded yields of such conventional oilseed crops as soybean (170 to 204 g m^{-2}) and sunflower (102 to 159 g m^{-2}) grown in the United States on freshwater (*9*).

At least five samples of seed from each harvest were analyzed (Table 2). Oil content ranged from 26 to 33% and protein ranged from 30 to 33%, whereas ash and fiber contents were both low, 5 to 7%. The oil was high in polyunsaturated fatty acids, particularly linoleic acid, which accounted for 73 to 75% of the oil. Austenfeld (*10*) found similar percentages of oil content and fatty acids in *S. europaea* L. seeds but reported an average seed weight of only 0.271 mg.

Five batches of seed (30 kg each) were extracted in solvent by a procedure similar to cottonseed milling with the use of pilot plant equipment (*11*). Seeds were flaked by rolling to a thickness of about 0.03 cm, then extracted with hexane in a continuous countercurrent extractor. The yield of crude oil was 28.6% (SD, 0.6%) and the remaining meal contained 5.5% oil (SD, 0.5%), 43.5% protein (SD, 0.7%), and 8.7% ash (SD, 0.3%; 75% NaCl).

The oil and meal were compared to soybean oil and meal at levels at which these types of ingredients are normally added to chicken starter diets as sources of calories and protein, respectively (Table 3). The two oils were comparable in caloric value but *S. bigelovii* meal contained an antigrowth factor or factors that reduced the growth rate and decreased the feed conversion efficiency compared to soybean meal. Three lines of evidence suggested that saponins in the seed meal were responsible for the growth inhibition. First, the seeds contained about 2% saponin based on the hemolytic activity and

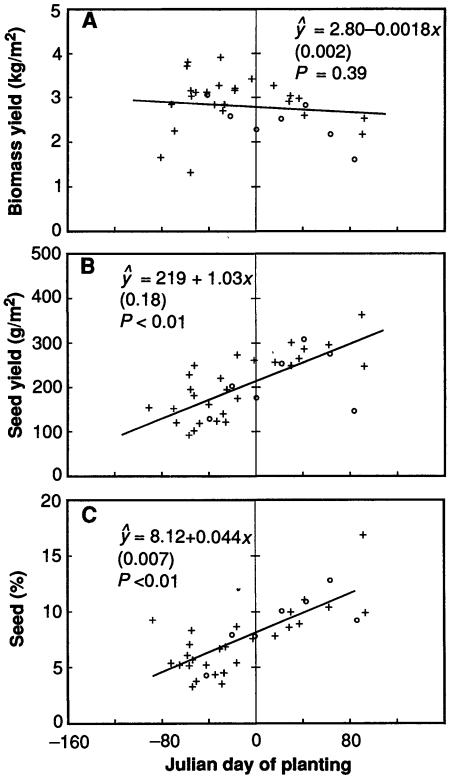

Fig. 1. Dry weight yields of (**A**) biomass, (**B**) seed, and (**C**) percentage of seed of *Salicornia bigelovii* as a function of planting date at Puerto Peñasco. The 1982 data (+) were from 27 individual plots planted on different dates in field 1; the 1984 data (○) were from seven strips planted at 3-week intervals within a single plot in field 2. The planting dates are plotted according to the Julian calender in which 31 December is day 0. The individual data points are the mean of three 1-m^2 quadants per plot or strip. Differences in slopes and means of values for 1982 and 1984 were not statistically significant and pooled regression analyses are shown with the standard error of the regression coefficient in parentheses.

Table 3. *Salicornia bigelovii* seed oil and meal compared to soybean oil and meal in chicken diets. Diets were composed according to data in (*19*). The control diet contained 2% soybean oil and 18% soybean meal. *Salicornia bigelovii* oil replaced soybean oil in one experiment. In other experiments, *S. bigelovii* meal replaced soybean meal at 14% of the diet (plus 4% soybean meal to balance protein and essential amino acid requirements). *Salicornia bigelovii* meal was tested unamended, supplemented with 1% cholesterol to counteract saponins, or extracted from seeds washed in NaOH to deactivate saponins (*14*) suspected to be in the meal. Each experiment contained six replications with eight birds for each diet tested. Birds were 1 to 9 days old at the start of experiments, which lasted 14 to 28 days. Relative growth rates (RGR) in grams per gram per day were calculated from the initial and final weights of chickens using the formula for exponential growth. Feed conversion ratios (FCR) were calculated from their total weight gain and the total feed consumed. The table shows the number of separate experiments in which a diet was tested (*n*), the mean and standard deviation (in parentheses) of RGR and FCR among experiments, and the percentage of RGR for test diets compared to the controls with which they were paired.

Diet	*n*	RGR	FCR	RGR (%)
All controls	7	0.130 (0.022)	1.50 (0.19)	100.0
2% *S. bigelovii* oil	1	0.104	1.74	102.0
14% *S. bigelovii* meal	6	0.072* (0.017)	2.42* (0.54)	56.3
14% *S. bigelovii* meal (NaOH-washed)	4	0.117 (0.016)	1.56 (0.33)	87.2
14% *S. bigelovii* meal (+1% cholesterol)	3	0.140 (0.002)	1.38 (0.06)	98.4

*Statistically significant difference from control at $P < 0.05$ with the Bonferroni *t* test. The treatments were compared with the total set of control experiments given in the table.

thin-layer chromatography of EtOH extracts from seeds (*12*). Second, the saponin antagonist, cholesterol (*13*), added to the chick diet at 1%, reversed the growth inhibition of *S. bigelovii* meal. Third, soaking the seeds in 1% NaOH before meal extraction deactivated the anti-growth factor or factors, similar to the finding of saponin detoxification by NaOH treatment in Kochia seeds (*14*). The unamended meal may be suitable for swine or ruminants that are less sensitive to saponins than poultry (*15*).

The areas of greatest demand for oilseed imports (*16*) coincide with some of the greatest expanses of subtropical coastal desert (*17*). *Salicornia bigelovii* appears to be a potentially valuable new high-yielding oilseed crop for these regions, yielding a vegetable oil high in unsaturated fatty acids, which is amenable to commercial oilseed extraction methods.

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Characterization of a Dimerization Motif in AP-2 and Its Function in Heterologous DNA-Binding Proteins

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The mammalian transcription factor AP-2 is a retinoic acid inducible sequence-specific DNA-binding protein that is developmentally regulated. In this report, the functional domains necessary for AP-2 DNA binding were studied. AP-2 required a dimerization domain and an adjacent region of net basic charge to achieve a sequence-specific protein:DNA interaction. The sequences responsible for dimerization consisted of two putative amphipathic alpha helices separated by a large intervening span region. This helix-span-helix (HSH) domain was unable to bind DNA when separated from the basic region, but was still capable of dimerization. The ability of the HSH domain to function as a module that promotes DNA binding through dimerization was further demonstrated by attaching it to the heterologous basic region of the c-Jun proto-oncogene product. The resulting chimeric protein specifically recognized an AP-1 DNA-binding site in the absence of an intact c-Jun leucine repeat and in a manner that was dependent on the presence of a functional AP-2 dimerization domain.

SEQUENCE-SPECIFIC DNA-BINDING proteins provide a fundamental mechanism for the regulation of transcription. Analysis of these proteins has indicated that they are often modular in nature, containing separate domains for DNA binding and transcriptional activation (*1*). Several transcription factors also possess dimerization domains, which are essential for DNA binding and may modulate the activity of the protein via complex formation (*2*). Recent studies have indicated the importance of amphipathic α-helices for these protein:protein interactions. Members of the bZIP family of proteins, including c-Jun, c-Fos, and C/EBP, dimerize via a single amphipathic α-helix (*2–7*) that has a heptad repeat of leucine residues on one face of the helix ("leucine zipper"). An alternative arrangement that promotes dimerization consists of two putative amphipathic helices separated by a short loop of 10 to 25 amino acids. This helix-loop-helix (HLH) motif is found in a number of DNA-binding proteins, including myoD, E12, TFE3, achaete scute, daughterless, and AP-4 (*8*).

The mammalian transcription factor AP-2 binds to a cyclic adenosine monophosphate (cAMP) and phorbol ester inducible sequence motif found in the cis-regulatory regions of several viral and cellular genes (*9*). The concentration of AP-2 is regulated temporally and spatially during development and is induced by retinoic acid treatment of teratocarcinoma cells (*10, 11*). AP-2 contains a COOH-terminal region of ~200 amino acids that is responsible for both DNA binding and dimerization of the protein in solution (*12*). The AP-2 DNA-binding region is organized in a manner similar to basic region–leucine zipper (bZIP) and HLH proteins, with a stretch of net basic charge adjacent to an area that is predicted to have an α-helical structure (Fig. 1). Examination of this potentially helical region reveals the presence of two amphipathic α-helices separated by a span of ~80 amino acids (Fig. 2).

To determine the contribution of this predicted helix-span-helix (HSH) structure to protein:protein interaction, we constructed a series of internal deletion mutants within the DNA-binding domain. The ability of

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