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The Rush Ranch Open Space Preserve (Rush Ranch) is located at the northwestern edge of the Potrero Hills and includes the largest remaining undiked tidal wetland within the Suisun Marsh region of the San Francisco Estuary. The brackish tidal wetlands grade into the transitional vegetation and undeveloped grasslands of the Potrero Hills, and we describe diverse vegetation that reflects the estuarine position, land use history, and hydrogeomorphic complexity of the site.

We present a useful framework for future study of vegetation at this San Francisco Bay National Estuarine Research Reserve site. Rush Ranch includes four major estuarine geomorphic units that are widely distributed in the region and support vegetation: subtidal channel beds, fringing tidal marsh, tidal marsh plain and tidal marsh–terrestrial ecotone. These are distinguished by small variations in hydrology and elevation, as noted and described through field observations and historic vegetation-mapping data. We discuss vegetation within each of these landforms, considering each vegetation community as a function of changing physical environment and biological interactions. Past land use and exotic plant species invasions have substantially altered Rush Ranch's tidal marsh vegetation patterns. Our results indicate 27% of the current estuarine wetland-associated flora at Rush Ranch are exotic species, and several are highly invasive. Despite these influences, Rush Ranch's position in the landscape provides important and increasingly rare habitat linkages between the tidal marsh and upland grasslands, which allows great potential for restoration and enhancement. We present a detailed flora and vegetation analysis by hydrogeomorphic setting to provide an ecological framework for future monitoring, research, and adaptive conservation management at Rush Ranch.

**Supporting material:**

Partial Flora of Estuarine Vegetation at Rush Ranch, Suisun Marsh, Solano Co., California

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# Estuarine Vegetation at Rush Ranch Open Space Preserve, San Franciso Bay National Estuarine Research Reserve, California

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## ABSTRACT

The Rush Ranch Open Space Preserve (Rush Ranch) is located at the northwestern edge of the Potrero Hills and includes the largest remaining undiked tidal wetland within the Suisun Marsh region of the San Francisco Estuary. The brackish tidal wetlands grade into the transitional vegetation and undeveloped grasslands of the Potrero Hills, and we describe diverse vegetation that reflects the estuarine position, land use history, and hydrogeomorphic complexity of the site.

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## KEY WORDS

Suisun Marsh, estuarine wetlands, tidal wetlands, brackish marsh, wetland flora, invasive species, plant community, vegetation, anthropogenic drivers

## INTRODUCTION

The 425 ha of estuarine wetlands at the Rush Ranch Open Space Preserve (Rush Ranch), a component site of the San Francisco Bay National Estuarine Research Reserve (NERR), are part of the largest extant tidal marsh within the brackish Suisun Marsh reach of the San Francisco Estuary (the estuary) (Figure 1). The tidal wetland at Rush Ranch is unique because of its areal extent, largely intact prehistoric marsh platform, hydrogeomorphic complexity, continuity between tidal marsh ecotones and undeveloped grasslands, and habitat provision for endangered and endemic plant populations.

Hydrology and geomorphology are fundamental determinants of the structure, dynamics, and productivity of wetland plant communities. The estuarine vegetation at Rush Ranch reflects hydrological influences on different spatial and temporal scales: (1) regional scale—location in the estuary; (2) temporal scale—historic land use; and (3) local scale—modern patterns of site-specific hydrogeomorphology. Rush Ranch is approximately 80 km up-estuary from the Golden Gate tidal inlet in the northern region of Suisun Marsh. Suisun Marsh is situated in between the extensive Sacramento–San Joaquin Delta (the Delta) and the North and South Bay reaches of the San Francisco Estuary. In this region, the hydrology and tidal mixing of fresh and salt water have been spatially and temporally dynamic, and historic variability in physical processes was a key driver of historic biological diversity (Moyle and others 2010). At the regional scale, the diversity of vegetation within the entire Suisun Marsh—and particularly at Rush Ranch—results from a combination of, and small

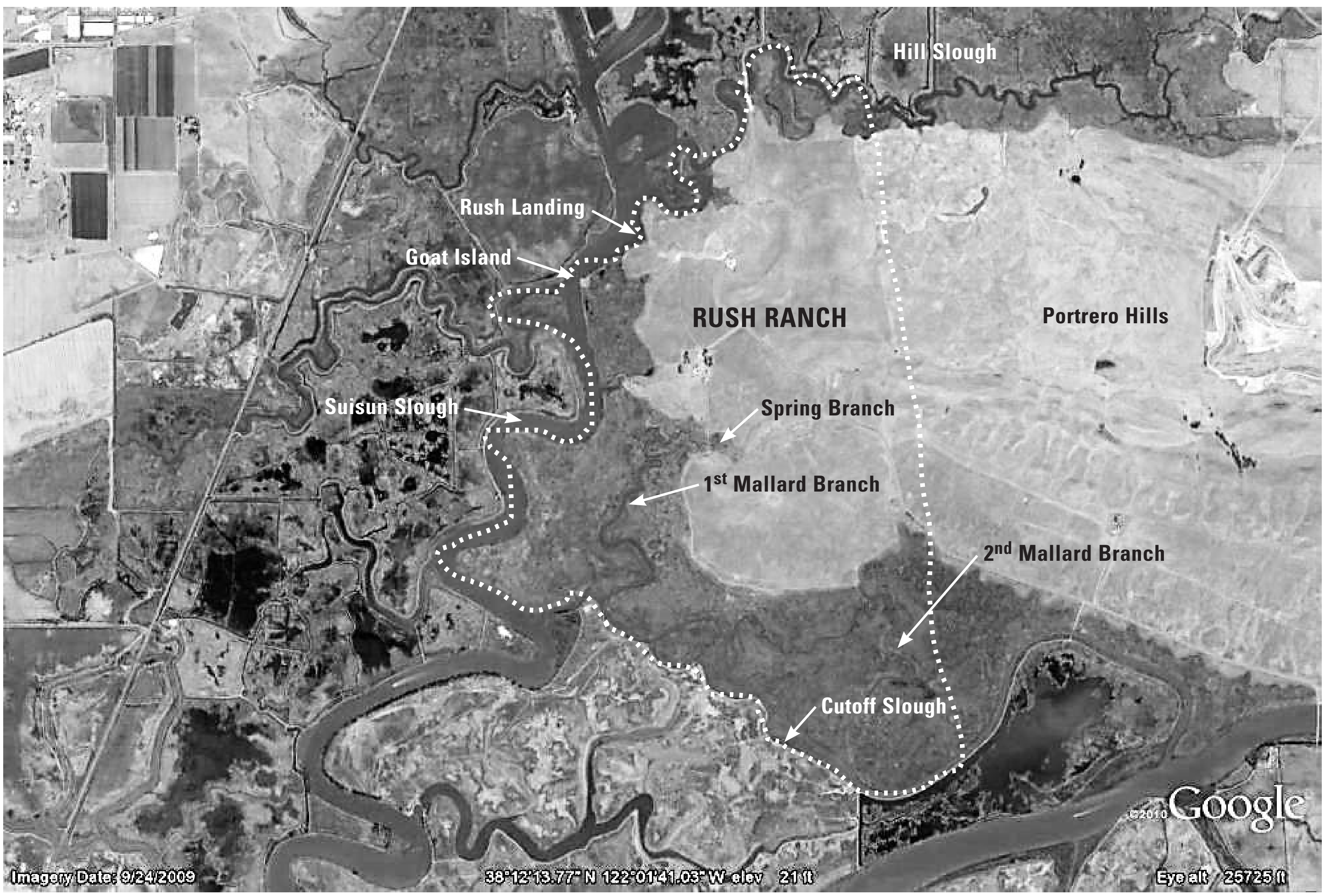


**Figure 1** Location of the Rush Ranch Open Space Preserve (838 ha, boundary in dotted line) (38°12′31.7″N Latitude, 122°1′31.9″W Longitude). Key tidal sloughs and landmarks within RROSP are identified. © 2011 Google

variations in, physical and geological factors, such as distance from the ocean; the magnitude of freshwater input from direct precipitation, watershed runoff, and Delta outflow; salinity pulses; storms; and the duration of tidal submergence (Atwater and others 1979; Josselyn 1983). In contrast to wetlands in the Delta, estuarine vegetation at Rush Ranch is influenced by large annual and interannual ranges in salinity (Moyle and others 2010). In recent times, key physical and chemical processes have been anthropogenically mediated by active management of Delta outflow and Suisun Marsh salinity regimes by state and federal water projects (Enright and Culberson 2009) that effectively reduce biologically important environmental variation (Moyle and others 2010).

The distribution and abundance of plant species and how these two factors change with hydrogeomorphic complexity are also influenced by the functional traits of plant species (Bonin and Zedler 2008; Shipley 2010). The site includes a rich estuarine flora that corresponds to unique hydrogeomorphic features within the marsh, and supports estuary-dependent wildlife and complex food webs. This vegetation is quite different from graminoid-dominated tidal marshes of the North American Atlantic Coast, and the brackish plant community composition and structure is also floristically distinct from, and more diverse than, tidal marsh vegetation in San Francisco Bay or along the outer coast of California (Mason 1972; Baye and others 2000; Grewell and others 2007; Watson and Byrne 2009). While the tidal wetlands and terrestrial–ecotone vegetation at Rush Ranch are unique and largely intact as compared to most of the San Francisco Estuary, they have not been immune to change, and do not represent a static, pre-development condition. They have a legacy of agricultural and ranching use, hydrologic modifications, and alteration to vegetation (Wetlands and Water Resources, Inc. 2011). As a result of this anthropogenic activity, the flora of terrestrial ecotones between estuarine marshes and uplands has been significantly degraded, and native flora from these areas is now regionally rare or extirpated (Baye and others 2000). Despite historic alterations, the estuarine plant communities at Rush Ranch are a significant natural resource that merit conservation attention. Rush Ranch has one of the only remaining gently sloping, undeveloped lowlands (alluvial fan topography and soils lacking intensive agriculture or urban or industrial development) bordering undiked tidal marsh. This setting provides rare geomorphic accommodation space for estuarine transgression as sea level rises, and a rare opportunity to conserve the high tidal marsh and its terrestrial ecotone.

Aspects of the tidal wetland vegetation of Suisun Marsh have been reviewed previously by Mason (1972), Atwater and Hedel (1976), Atwater and others (1979), Josselyn (1983), Wells and Goman (1995), Baye and others (2000), Hickson and others (2001), Byrne and others (2001), Grewell and others (2007), Watson and Byrne (2009), and Vasey and others (submitted). Floristic surveys and studies of plant ecology specific to Rush Ranch and contiguous tidal wetlands offsite have also contributed to our knowledge of the site (Wetland Research Associates 1990; Siegel 1993; Ruygt 1994; Grewell 1996; Grewell and others 2003; Fiedler and Keever 2003; Fiedler and others 2007; Grewell 2008a; Watson and Byrne 2009; Reynolds and Boyer 2010). These surveys and studies suggest that the modern vegetation at Rush Ranch is typical of relict tidal wetlands elsewhere in the Suisun Marsh, and though rare species and plant assemblages occur, the Rush Ranch flora shares many elements of wetland flora with marshes elsewhere in the San Francisco Estuary and along northern coastal California.

This profile presents historical context, descriptions and baseline data on the floristic composition and ecology of estuarine vegetation at Rush Ranch, the relationship of vegetation to hydrogeomorphic settings and associated hydrologic and other physical–chemical processes, as well as modern transformations of vegetation pattern. In addition, we provide a framework for future monitoring, research, and adaptive conservation management.

## GEOMORPHIC AND HISTORIC DEVELOPMENT OF VEGETATION

### Paleoecology and Historical Ecology

In addition to spatial scale differences in hydrology, past land use exerts great influence on hydrology, and thus on present plant community structure. Paleoecological reconstructions of geology, climate, sedimentation, and vegetation change of the northern San Francisco Bay Estuary during the past 7,000 years have included site-specific studies of the tidal wetlands that ring the Potrero Hills (including Rush Ranch), which are the ecological heritage of modern vegetation. The oldest tidal brackish and salt marsh sediments in the northern San Francisco Bay estuary are associated with a slowing of post-glacial sea level rise rates as they approached modern sea level. This initial deceleration of sea level rise began 6,000 yr before present (BP), and by approximately 4,000 yr BP, initiation of most modern tidal marsh plains began, although some emergent fresh–brackish estuarine marshes deposited discontinuously earlier (Wells and others 1997; Malamud–Roam and Ingram 2004; Malamud–Roam and others 2007). Studies of the stratigraphic record of microfossils (pollen, diatoms, foraminifera) and organic and inorganic sediments at Rush Ranch indicate that the wetland vegetation at Rush Ranch developed and has been subjected to strong environmental variability over millennial and centennial scales, as well as climate-driven changes in hydrology and aqueous salinity (Wells and others 1997; Malamud–Roam and Ingram 2004; Malamud–Roam and others 2007). These climate variations occurred amid a background of relatively slow and stable sea-level rise rates. They corresponded with marked fluctuations in the composition of tidal marsh dominant vegetation, indicated by reversals in relative abundance and composition of pollen assemblages corresponding with low- and high-salinity regimes (Byrne and others 2001).

Empirical reconstruction of Rush Ranch paleoecology clearly indicates that the existing mature marsh plain and sloughs, and corresponding development and evolution of marsh plant communities, have a relatively brief geologic existence—less than two thousand years—and underwent profound fluctuations in vegetation dominance and salinity regimes, as well as in precipitation (Byrne and others 2001). The stratigraphic and pollen records do not support the assumption of an “equilibrium” or steady “natural” state in either Suisun Marsh or Rush Ranch (Byrne and others 2001; Goman and others 2008). These records have specific implications for special-status species conservation, particularly endemic Suisun Marsh species. Suisun Marsh historic endemic species, some of which are now endemic to Rush Ranch alone or nearly so, either persisted in refugial habitats within local salinity gradients of Suisun Marsh, or underwent range shifts very rapidly between Suisun Marsh, the western estuary, and the Delta. Stable, suitable habitat likely did not persist at any one location at Rush Ranch for more than a thousand years.

## Early Anthropogenic Influences on Estuarine Vegetation

Rush Ranch is located near some of the largest prehistoric Patwin (Wintun) village sites recorded in the Suisun Marsh region (Kroeber 1925; Johnson 1978; Fulgham Archaeological Resource Service 1990). Patwin and California Indians inhabiting the estuary’s margins used annual burning of grasslands and after-seed harvest in the lowland valleys for hunting, maintenance of favorable seed (pinole), and bulb production (Bean and Lawton 1973; Lewis 1973; Johnson 1978; Lightfoot and Parrish 2009). Annual burns likely influenced the character of tidal marsh edges and stream valleys, particularly in limiting the development of woody scrub. In addition to burning activities, digging, stem cutting, and burning of tule stands to enhance growth also likely altered productivity and the ecology of tidal marsh vegetation in California (Anderson 2005). *Schoenoplectus acutus* (hardstem bulrush), *S. californicus* (California bulrush), *Juncus* sp., *Carex barbarae* (basket sedge) and other sedge beds were harvested for textiles (house construction, reed boats, clothing, footwear, duck decoys, and basketry) as well as for food (Johnson 1978; Anderson 2005). In the 1700s, Spanish explorers also introduced both non-native plants and fire into the system. All of these activities potentially influenced the structure of tidal marsh vegetation at Rush Ranch.

Photographs and other records from the late 19th and early 20th centuries suggest that historic anthropogenic influences on Rush Ranch tidal marshes include: regional and local diking, (e.g., Suisun Slough and partial diking within the marsh plain, the Second Mallard Branch drainage), ditching to drain tidal marsh plains (mosquito ditching), haying and livestock grazing in tidal marsh, creation of tidal marsh pans and ponds, construction of slough dams and partial levees along marsh perimeters, and introduction of non-native animal and plant species. These alterations contributed to indirect ecological alterations such as increased terrigenous sedimentation from gullies and seasonal streams, and to slope failures of adjacent hillslopes, both subject to overgrazing.

Diking of historic tidal marsh in the Suisun region progressed from the late 1870s through the 1970s. The construction of full and incomplete dikes at Rush Ranch along slough borders of tidal marshes likely contributed significantly to local declines in tidal slough bank vegetation (including rare endemic plants) that was regionally decimated by early 20th century diking. Diking and ditching, and cattle manure in the tidal marsh, also likely facilitated the spread of invasive non-native species into the marsh. Diking of historic tidal marsh has greatly affected estuarine ecotone transitions in the San Francisco Estuary by creating sharp boundaries between wetlands and terrestrial grasslands (Josselyn 1983; Fieldler and Zebell 1995). Mason (1972) and George and others (1965) report accounts from "old timers" that before wetlands in Suisun Marsh were diked, there were extensive tidal marshes "where water stood on the land," and tall tules lined the margins in deeper water. This pattern of vegetation was also reported by DeAnza as he first sailed through Suisun Bay in 1776. Historical reports also note that high marsh plains on Grizzly Island were covered with *Distichlis spicata*, which was dominant but associated with salt-tolerant species including *Sarcocornia pacifica* (syn. *Salicornia virginica*, *Sarcocornia pacifica*, perennial pickleweed) in poorly drained areas (George and others 1965; Mason 1972).

In the 19th century, *D. spicata* (salt grass) and *Schoenoplectus americanus* (chairmaker's bulrush) were both harvested as commodities and utilized as packing material by the Gladdin McBean Pottery Works in Lincoln (Frost, not dated). Saltgrass hay bales were also loaded onto schooners at sites such as Rush Landing, and transported for sale as cattle feed (Mason 1957, 1972; George and others 1965; Frost, not dated). Haying directly in tidal marshes also likely had acute and prolonged inhibitory effects on reproduction of what are now rare, endemic high tidal marsh plants.

Grazing most likely had effects similar to those discussed for haying. Grazing in marshes would likely have been most intensive in early summer, when hillslopes are dry, and green forage is restricted to wetlands. Intensive grazing likely occurred during peak flowering periods of *Cirsium hydrophilum* var. *hydrophilum* (Suisun thistle) and *Chloropyron molle* subsp. *molle* (soft bird's beak), for example. Cattle grazing has been officially excluded from tidal wetland areas of Rush Ranch since the Open Space Preserve was established (Wetland Resource Associates 1990), but in the 1980s, before transfer of ownership to Solano Land Trust (SLT), grazing and burning within the tidal wetland was pervasive (Peter Moyle, University of California, Davis, pers. comm., 2011). After cattle were removed from the marsh, endangered *C. h.* var. *hydrophilum* (presumed extinct) recruited and spread along tidal creek channels (Brenda Grewell, pers. obs., photo-documented in Figure 2). Since SLT ownership, there has been both unintentional and intentional grazing of cattle and horses within tidal marsh areas, and the practice has recently (2010–2011) been re-established (Ken Poerner, Solano Land Trust, pers. comm., 2011). Cattle grazing has directly affected endangered plant populations in the tidal wetlands, and the resultant trampling destroyed a historic population of endangered *C. m.* subsp.*molle* in the marsh (Grewell and others 2003; Grewell 2005).

Historic hunting influences on Rush Ranch and the surrounding private hunting clubs and public wildlife areas also influenced tidal wetland vegetation within Rush Ranch. Much of the historically abundant native vegetation (e.g., *S. pacifica* and *D. spicata*) in Suisun Marsh was considered "undesirable" for waterfowl (Rollins 1981), and early management of diked wetlands focused on production of non-native plants and some native species (particularly *Bolboschoenus maritimus* [alkali bulrush], *Scirpus robustus* misapplied) that were not naturally dominant in the region (Miller and others 1975). Several plant species or novel genotypes of local species were introduced by duck clubs, who purchased plant propagules (seeds or tubers) for waterfowl habitat from eastern and southern U.S. sources and planted them in Suisun Marsh and other California wetlands (Mason 1957).

Releases of exotic ring-necked pheasants and other game birds on adjacent hunting lands may explain the high density of pheasants at Rush Ranch, where they are protected from hunting. Pheasants rely on plant seeds and insect food sources, and their foraging effects on Rush Ranch vegetation and native wildlife food webs are unknown. Feral pigs (*Sus scrofa*), a relative of the European boar ,are non-indigenous to North America and introduced for hunting; in recent years, they have invaded Rush Ranch tidal wetlands. Their effects on tidal marsh vegetation are quite visible, but their ecological effects have not been studied at Rush Ranch. Rooting and wallowing by feral pigs are a major source of unnatural disturbance in the marshlands. For example, large sections of *D. spicata*–dominated areas of marsh plains have been especially affected at the Open Space Preserve (Christine Whitcraft, Brenda Grewell and Peter Baye, pers. obs., 2000-2011). Habitat destruction by feral pigs is a major threat to the long- and short-term viability of endangered soft bird's beak (Grewell and others 2003) and endangered Suisun thistle (Fiedler and others 2007) at Rush Ranch.

## Exotic Plant Introductions

The introduction of exotic plant species and their subsequent spread and colonization as invasive weeds has degraded tidal wetlands of the San Francisco Estuary, and Rush Ranch has not been excluded from this effect. Interactions between exotic and native species alter the structure and function of wetland plant communities, profoundly affect the diversity and abundance of native flora, and pose significant challenges to the integrity and sustainability of current and proposed wetland restoration projects. At Rush Ranch, *Lepidium latifolium*, *Apium graveolens* and a suite of winter annual grasses—*Hainardia cylindrica* (syn. *Monerma cylindrica*, barbgrass, thintail, hardgrass), *Parapholis incurva* (sicklegrass), *Polypogon monspeliensis* (rabbitsfoot grass, annual beard grass)—have been particularly problematic, and directly affect endangered native flora (Grewell and others 2003; Grewell 2005; Fiedler and others 2007; Grewell and others 2007). Tidal wetland restoration sites are highly susceptible to weed invasion from hydrochorous dispersal of weed diaspores, the disturbed condition of newly restored sites, and also because the implementation of restoration projects is proceeding before regional eradication of weeds to manageable levels. Exotic, invasive plant species of particular concern at Rush Ranch are discussed below, and additional exotic plants with potential for increased spread and effect are listed in the Appendix.

***Lepidium latifolium:*** *L. latifolium* (perennial pepperweed, white top) was first was first discovered in California in 1936 (Robbins 1941). From 1986 to 1996, *L. latifolium* began rapidly and aggressively expanding its range, as water management and land use practices in the Delta changed dramatically (Mooney and others 1986; Howald 2000). In the early 1990s, *L. latifolium* invaded and spread in tidal wetlands, along ephemeral stream corridors, and in disturbed upland areas at Rush Ranch (Brenda Grewell, pers. obs., 1990–1991. By 1995, *L. latifolium* had aggressively displaced formerly dense stands of endangered *C. h.* var. *hydrophilum* (Brenda Grewell, pers. obs., photo documented in Figure 2). At Rush Ranch, several plant and animal species, including endangered endemic taxa, co-exist with the weed as understory species (Spautz and Nur 2004; Reynolds and Boyer 2010). In 2003, *L. latifolium* was the third most frequent plant associate (85% frequency) of endangered *C. h.* var. *hydrophilum* at Rush Ranch (Fiedler and others 2007). By 2005, *L. latifolium* had invaded 12% of population patches of endangered soft bird's-beak that had been reintroduced at Rush Ranch in 2000 (Grewell 2005). This aggressive weed threatens the viability and recovery of endangered plant populations at Rush Ranch and elsewhere in San Francisco Estuary (Grewell 2005; Fiedler and others 2007).

***Apium graveolens:*** *A. graveolens* (celery), a horticultural–garden escapee native to Europe, has invaded estuarine emergent wetland plant communities at Rush Ranch, greater Suisun Marsh, and the Carquinez


**Figure 2** In 1992, after historic cattle grazing ceased in Rush Ranch tidal wetlands, *Cirsium hydrophilum* var. *hydrophilum* (previously considered extinct) rebounded, and was observed as a robust, dominant plant species along first-order tidal creeks at Rush Ranch. By 1995, the exponential spread of *Lepidium latifolium* was underway along the same tidal creek, and *C. h.* var. *hydrophilum* was reduced in stature and abundance within the community.

Straits. Jepson (1923) and Mason (1957) noted the naturalization of *A. graveolens* in marshes and along streams in the Sacramento Valley and southern California. The species was described as common in the San Francisco Estuary more than 30 years ago (Atwater and others 1979), but invasive spread has been recent. In its native European range (Spain), relative cover and elevational amplitude of *A. graveolens* are low relative to other salt marsh plant community members, and the plant is restricted to high marsh (Sánchez and others 1996). At Rush Ranch, *A. graveolens* is often closely associated with *Lepidium latifolium*, but it has a broader ecological amplitude than its co-invader, and occupies a broader range of hydrogeomorphic settings than has been reported from its native range (Brenda Grewell, pers. obs.). Within 4 years of an experimental restoration of *C. molle* subsp. *molle* to the Spring Branch restoration site at Rush Ranch, *A. graveolens* had invaded *C. molle* subsp. *molle* sub-populations, and its frequency of occurrence was 18% (Grewell 2005). The frequency of *A. graveolens* with endangered *C. h.* var. *hydrophilum* was as high (85%) as that of its co-invader, *L. latifolium*, at Rush Ranch (Fiedler and others 2003). The invasive populations in the Potrero Hills region may be a source for new invasions westward in the estuary. In 2009, *A. graveolens* first colonized the Southampton Marsh Preserve (Benicia State

Recreation Area) in the Carquinez Straits, suggesting the need for greater recognition of this problematic invasive plant, and management and reduction of upstream source populations (Grewell 2010).

**Exotic annual grasses.** A suite of exotic, winter annual grasses are invasive on the high marsh plain near the terrestrial ecotone, and also in seasonal wetlands at Rush Ranch. *Polypogon monspeliensis* is native to Europe, Asia, and Africa. Evidence from adobe brick remains place the introduction of *P. monspeliensis* to California during the mid-19th century (Frenkel 1977). Seasonally low salinity levels imposed by winter and anthropogenic runoff into estuarine wetlands control the distribution and abundance of *P. monspeliensis* (Callaway and Zedler 1998) because germination percentages of seeds decrease with increasing salinity. Thus, salt applications may be a practical control method (Kuhn and Zedler 1997). *H. cylindrica* and *Parapholis incurva* (curved sicklegrass) are taxonomically similar, European introductions. *H. cylindrica* is locally abundant in terrestrial ecotone and turf pans, Hill Slough and Rush Ranch tidal marshes (Peter Baye and Brenda Grewell, pers. obs.). *P. incurva* is less common at Rush Ranch and other tidal wetlands ringing the Potrero Hills, but locally co-occurs with *H. cylindrica* (Peter Baye and Brenda Grewell, pers. obs.).

The exotic, cool-season grasses all have a C3 photosynthetic pathway, and the inherent lower photosynthetic rate suggests they will be competitively inferior in interactions with C4 grasses such as native *D. spicata* (Waller and Lewis 1979). At Rush Ranch, *D. spicata* is obviously more abundant than these exotic cool-season grasses. However, in a management context, competitive superiority and relative abundance are not the only criteria by which exotic species should be considered. At Rush Ranch, seeds of these exotic grasses germinate from late November to February, and the exotic, annual grasses complete their annual growth cycle by late spring to early summer. During the pre-reproductive growth phase of the exotic annuals, the endangered hemiparasitic herb, *C. m.* subsp. *molle* (Figure 3) germinates and emerges as a seedling in exotic grass-occupied habitat, and forms parasitic connections with the roots of the exotic grasses, the exotic hosts die back when *C. m.* subsp. *molle* is in seedling stage (Grewell 2004). In a field study at Rush Ranch and Hill Slough, nearest neighboring plant species (potential hosts) were shown to greatly affect *C. m.* subsp. *molle* seedling survivorship, and the presence of winter exotic grasses (particularly *H. cylindrica*) in the community is highly correlated with premature mortality of the endangered plant seedlings; survivorship was highest when native *D. spicata* and *S. pacifica* were nearest neighbors (Grewell and others 2003; Grewell 2004). These results suggest that control of exotic winter grasses in estuarine vegetation at Rush Ranch and elsewhere, before restoration attempts, is essential for sustainable populations of *C. m.* subsp. *molle* (Grewell 2004, 2005). When non-native species removal is given priority in estuarine wetlands,

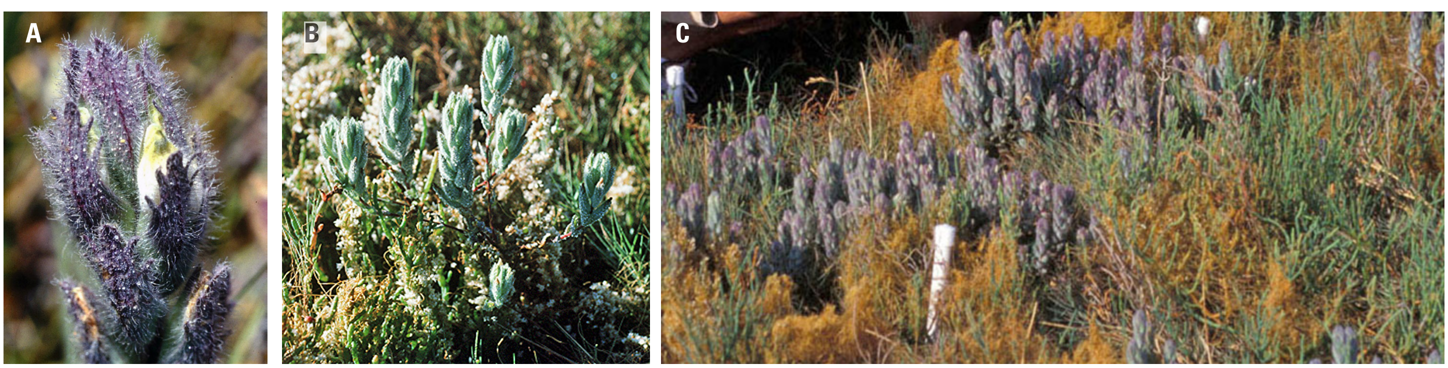


**Figure 3** The endangered *hemiparasite Chloropyron molle* ssp. *molle* (soft bird's beak, A) often occurs with the holoparasitic vine *Cuscuta pacifica* var. *pacifica* (salt marsh dodder), and is dependent on native halophytes such as *Sarcocornia pacifica* (B) and *Distichlis spicata* (C), to complete its annual life cycle at Rush Ranch.

the negative effects of non-native host plants suggest that the costs of non-competitive mechanisms must be considered during the recovery (Fellows and Zedler 2005; Grewell 2005).

***Phragmites australis.*** Cosmopolitan *Phragmites australis* (common reed) is a large, perennial grass with creeping rhizomes and stolons that is found worldwide. Two recognized subspecies of *P. australis* (one native, the other exotic) are among the most misunderstood plant taxa in Suisun Marsh and at Rush Ranch. Fossil records dating to the Cretaceous and additional archeological records confirm a long presence of *P. australis* in North America as a minor native component of tidal wetland plant communities (Orson and others 1987). In the past 150 years, a dramatic expansion of *P. australis* in North America has occurred to the point that it is considered a nuisance in many estuaries. This aggressive spread by vegetative growth may have both environmental and genetic causes, and multiple karyotypes are involved (Chambers and others 1999). Molecular studies have confirmed native, introduced, and Gulf Coast North American *Phragmites* lineages are genetically distinct, and invasive introduced populations do not represent a hybrid population type (Saltonstall 2003a). Native individuals persist in many midwestern and western states, including California, but introduced populations are also present, and recently introduced genotypes largely dominate the Atlantic coast region (Saltonstall 2003b).

The typically non-invasive genotype *Phragmites australis* (Cav.) Steud. subsp. *berlandieri* (E. Fourn.) Saltonstall & Hauber, native to California, is present at Rush Ranch, nearby Peytonia Slough Ecological Reserve, and other tidal wetlands in the Delta and Suisun Marsh (Brenda Grewell and Art Shapiro, UC Davis, pers. obs., 1998). This native taxon serves as host plant for *Ochlodes yuma* (Yuma skipper), which is only associated with the native genotype. The exotic, invasive genotype, *P. australis* subsp. *americanus*, has been adopted by *Poanes biator* (broad-winged skipper), a large eastern Lepidopteran species (Shapiro and Manolis 2007). In disturbed environments, both native and exotic genotypes can spread and displace competing macrophytes, though aggressive spread is more typical of the more recent, exotic invader. Differences between the two subspecies can be subtle, and may partially depend on ecological conditions, but there are distinguishing morphological characters (Swearingen and Saltonstall 2010). The assumption that all *P. australis* present is the invasive taxon can be problematic, because some stands at Rush Ranch have persisted for decades. The presence of the native genotype at Rush Ranch that supports native insect species should be considered in management plans.

## Importance of Vegetation Presence and Type

Coastal wetlands and their ecotones provide key ecological services and ecosystem functions (Emmett and others 2000; Levin and others 2001; Weslawski and others 2004). Many of these services and functions depend on the composition and structure of plant communities (Bruno and Bertness 2001). In estuarine communities, vascular plants act as the major modifiers of the physical environment, provide primary energy and nutrient sources, and form most of the structural environment for other organisms. Critical marsh functions (such as nursery habitat provision, bank stabilization, runoff filtration, and trophic support) are directly and indirectly tied to the presence of vascular plants (Gleason and others 1979; Warren and Niering 1993). At Rush Ranch and elsewhere within San Francisco Bay estuary, vegetation type and structure, as well as marsh size and surrounding land use, are important in determining the distribution of multiple bird species (Spautz and others 2006) and macroinvertebrate trophic relationships at nearby sites at Grizzly Island (de Szalay and Resh 1996). Thus, understanding and documenting the location and distribution of plants through time at properties such as Rush Ranch is essential to effective management and preservation of these ecologically important habitats.

## Contemporary Vegetation Patterns Relative to Hydrogeomorphic Settings

A wide range of environmental factors (i.e., hydroperiod, nutrient regimes, disturbance levels) and their interactions control the structure and composition of estuarine vegetation (Levine and others 1998; Keddy

2000). Tidal submergence is a complex measure that serves as the primary control of the elevational ranges of tidal marsh plant species (Hinde 1954; Atwater and others 1979; Macdonald 1988; Byrne and others 2001; Watson and others submitted). Plant functional traits that convey stress–avoidance or stress–tolerance ability combine with competitive and facilitative interactions among plant species to influence estuarine plant species presence and abundance across environmental gradients (Keddy 1990; Bertness 1992; Pennings and Bertness 2001; Grewell and others 2007; Grewell 2008a). At a local scale, the environmental heterogeneity associated with hydrogeomorphic complexity combines with past land use and location to support distinct plant communities and assemblages. Vegetation patterns in oligohaline to brackish marshes such as Rush Ranch are often more patchy (Crain 2008) than zonal, compared with tidal salt marshes, thus we will discuss vegetation patterns in a geomorphic landscape unit context. Geomorphic units are planning areas delineated on the basis of integrated topographic, vegetation, and hydrologic features. These landforms can serve as the basis of conceptual physical models for soil–vegetation distribution and dynamics, and are the major controls of habitat quality and spatial pattern of habitats over time. In addition, hydrogeomorphic units provide

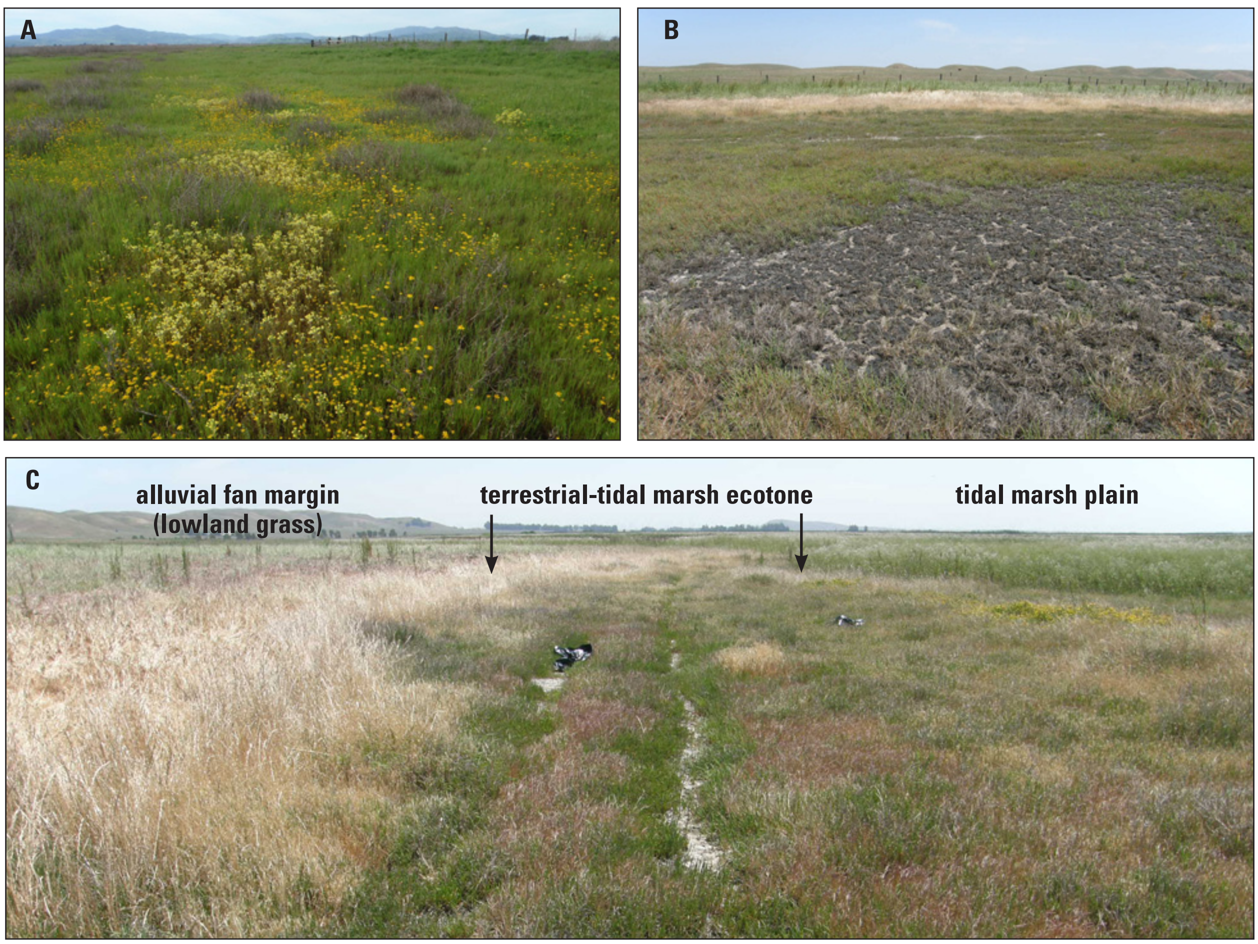


**Figure 4** High marsh-terrestrial ecotone along margins of alluvial fan dominated by lowland grassland south of Rush Ranch (Cutoff Slough marshes), forming high marsh pans that are similar to shallow saline seasonal wetlands subject to extreme high-tide flooding. Annual forbs *Lasthenia glabrata* (smooth goldfields), *Triphysaria versicolor* (owl's-clover) form conspicuous but ephemeral vernal wildflower displays (A). The ecotone desiccates in summer to (B) algal and cyanobacterial crusts and (C) dwarfed vegetation of turf pans (annual graminoids *Hordeum gussoneanum*, *Lolium perenne*, *Juncus bufonius*, with sparse low patches of *Triglochin concinna* and *Sarcocornia pacifica*).

an appropriate context for description of the azonal nature of modern vegetation at Rush Ranch.

Rush Ranch includes four major estuarine geomorphic units: subtidal channel beds, fringing tidal marsh, tidal marsh plain, and tidal marsh–terrestrial ecotone (Figures 4–7); and three major terrestrial geomorphic units (hillslopes, inactive and active alluvial fans). Our focus is on the diverse array of estuarine wetland vegetation and ecotonal vegetation at the margins of tidelands at Rush Ranch. Here we describe the plant communities of, subtidal channel beds, fringing tidal marsh, tidal marsh plain, tidal marsh ecotones, and tidal–terrestrial ecotones (including alluvial fans).

## SUBTIDAL CHANNEL BEDS

Submerged aquatic vegetation (SAV) includes rooted flowering plants that grow primarily below the water surface. The primary *Stuckenia pectinata* (syn. *Potamogeton pectinatus,* sago pondweed) and *Ruppia maritima* (widgeongrass) beds in San Francisco Estuary are around islands and other shallow areas in Honker Bay, Suisun Cutoff, and Suisun Bay (Schaeffer and others 2007; California State Coastal Conservancy 2010). *S. pectinata* and *R. maritima* have long been recognized as important waterfowl food plants in managed wetlands throughout Suisun Marsh (George and others 1965; Miller and others 1975). Important food plants from out-of-state sources were planted extensively by duck club managers on Honker and Suisun Bay islands and throughout Suisun Marsh (Miller and others 1975), and novel genotypes of *S. pectinata* and other waterfowl food plants may have been introduced and dispersed into Bay shallows (Mason 1957). Most SAV in the vicinity of Rush Ranch occurs in diked managed wetlands with perennial ponds and ditches, which in some years support substantial stands of *S. pectinata*, *R. maritima*, and *Zannichellia palustris* (horned-pondweed) (Mason 1972). *Stuckenia pectinata* typically dies back when water salinity exceeds 15 ppt (Kantrud 1990) but reappears with the return of oligohaline conditions. *Ruppia maritima* is an opportunistic species that thrives in warm and less saline water (Kantrud 1991; Koch and Dawes 1991), yet also tolerates salinity fluctuations and marine conditions. In 2010, extensive beds of *S. pectinata* appeared in open subtidal beds of Suisun Slough near Goat Island (Peter Baye, pers. obs., 2010), possibly in relation to declining suspended sediment supply and turbidity (Ganju and Schoelhammer 2009) and aqueous salinity (Moyle and others 2010).

## FRINGING TIDAL MARSH

Fringing tidal marsh is positioned immediately above typically unvegetated subtidal channel beds (Figures 5 and 6). This tidal marsh landform occurs as narrow bands on low edges of channels or at the edges of the marsh between “uplands” (hillslopes, scarps, alluvial fans) and tidal sloughs and appears to provide wave-damping, peat-forming, and sediment deposition functions comparable with high fringing marshes investigated in Maine (Morgan and others 2009). This landform supports plant species diversity and richness similar to (and in some locations, exceeding) vegetation of many high marsh plain areas at Rush Ranch. In contrast to the wave-attenuating marsh plains, fringing marshes of Rush Ranch are generally exposed to wind-waves from open slough fetch from the west and northwest. Fringing marsh occurs as narrow bands along the large, tidal sloughs (Suisun Slough and Hill Slough), particularly where the sloughs abut levee banks. Fringing marsh is also present where tidal sloughs border the neighboring hills with abrupt changes in slope that preclude development of tidal marsh plains (e.g. the reach of Suisun Slough immediately north of Rush Landing).

In fringing or narrow tracts of tidal marsh, sinuous, complex tidal drainage networks are not able to develop because of the insufficient area available, and the proximity of relatively steeper drainage gradients to the adjacent sloughs. Fringing marshes at Rush Ranch have developed extensively along the upland transition. Fringing marsh is also found in small, discontinuous segments that are directly exposed to wave action, which form dynamic peat slumps and scarps along slough edges. Fringing marsh may also be buffered by wave-damping, tule-dominated low marsh. These tule-dominated areas

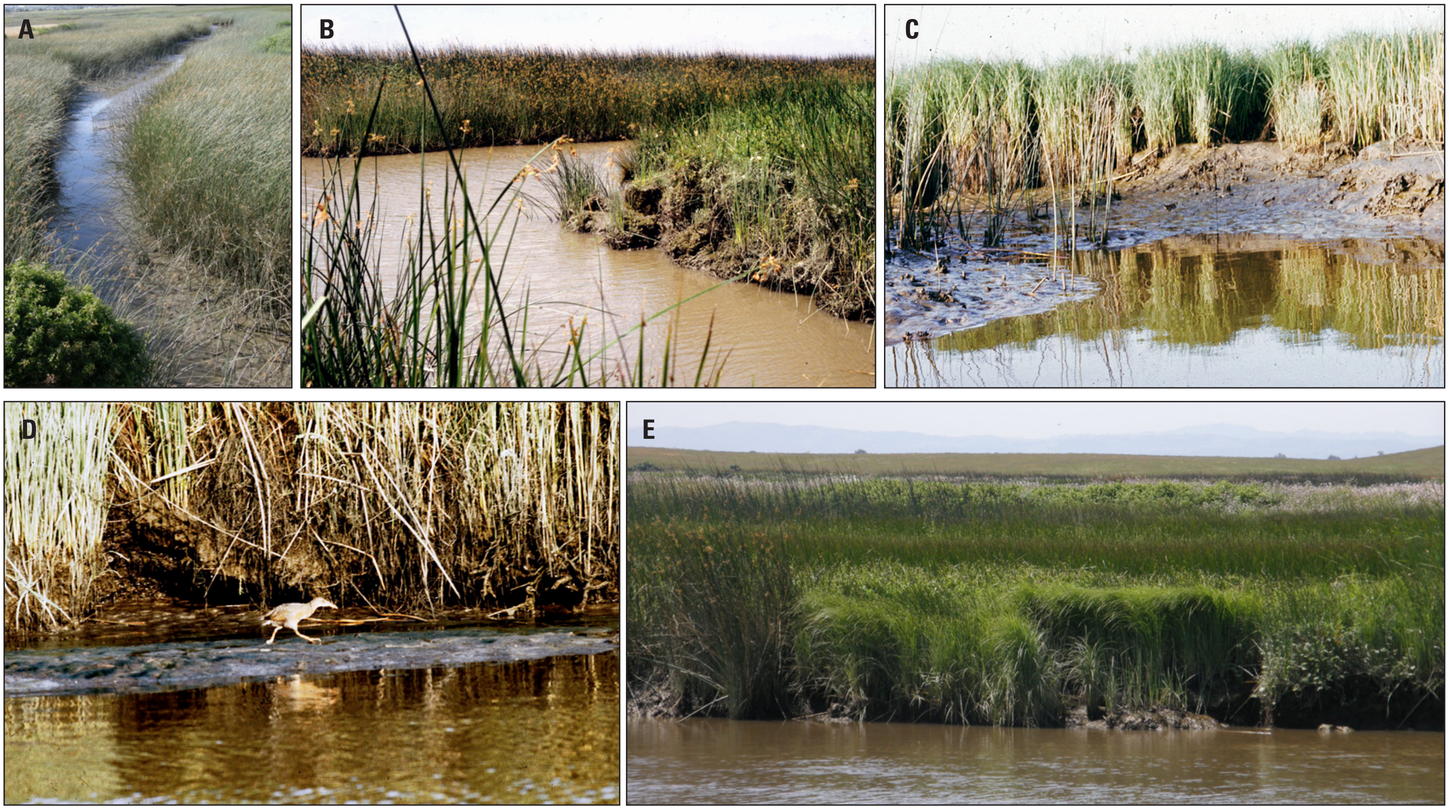


**Figure 5** Low tidal brackish marsh along mud banks of Rush Ranch tidal sloughs (First and Second Mallard Branches) are typically dominated by (A–D) tules (*Schoenoplectus californicus*, *S. acutus*) with cattails (*Typha latifolia*, *T. domingensis*) that provide cover and foraging habitat for California clapper rails (D), but fringing marsh also supports colonies of Lyngbye's sedge (*Carex lyngbyei*) along Hill Slough (E) and upper Suisun Slough.

may also serve as a barrier that can limit the growth and spread of adjacent marsh vegetation species toward tidal sloughs. Fringing marshes at Rush Ranch appear to have no history of ditching or diking, and are generally composed of mostly organic (peat or muck) fine sediment, except at edges of active or recently active alluvial fans, where better-drained mineral sediments are found. In some locations, substantial sediment has deposited along the exterior of artificial levees, allowing vegetation to colonize and expand outward for large distances into the slough. At Rush Ranch, fringing tidal marsh banks adjacent to dikes are steep scarps composed primarily of fine-grained peaty sediments. Fringing marshes adjacent to active alluvial fans or subject to slow current support limited natural levees with overbank deposits. These natural levees include better-drained sediments that support vegetation less tolerant of long hydroperiods.

The fringing marsh at Rush Ranch includes inundation-tolerant *Schoenoplectus–Typha–Carex* (bulrush–cattail–sedge) associations at lowest elevations. At middle to higher elevations, the fringe vegetation usually is composed of subshrubs, creeping perennial forbs and rushes, and grasses, as well as bunchgrasses that can exist in brackish salinity. Tall, shrubby *Grindelia stricta* var. *angustifolia* (syn. *G. hirsutula*, marsh gumplant) often borders tidal creek banks and provides dense emergent cover in mature tidal marshes (Baye 2007); it is also abundant in high fringing marsh. The vegetation typical of the widespread well-drained, high banks of mature tidal creeks of Rush Ranch is also abundant in high fringing marsh, including tall, dense growth forms of *S. pacifica*, *Frankenia salina* (alkali heath), *Potentilla anserina* var. *pacifica* (syn. *Argentina egedii*, silverweed, cinquefoil), *Glaux maritima* (sea-milkwort), *D. spicata*, *Deschampsia cespitosa* (L.) subsp. *hol-*

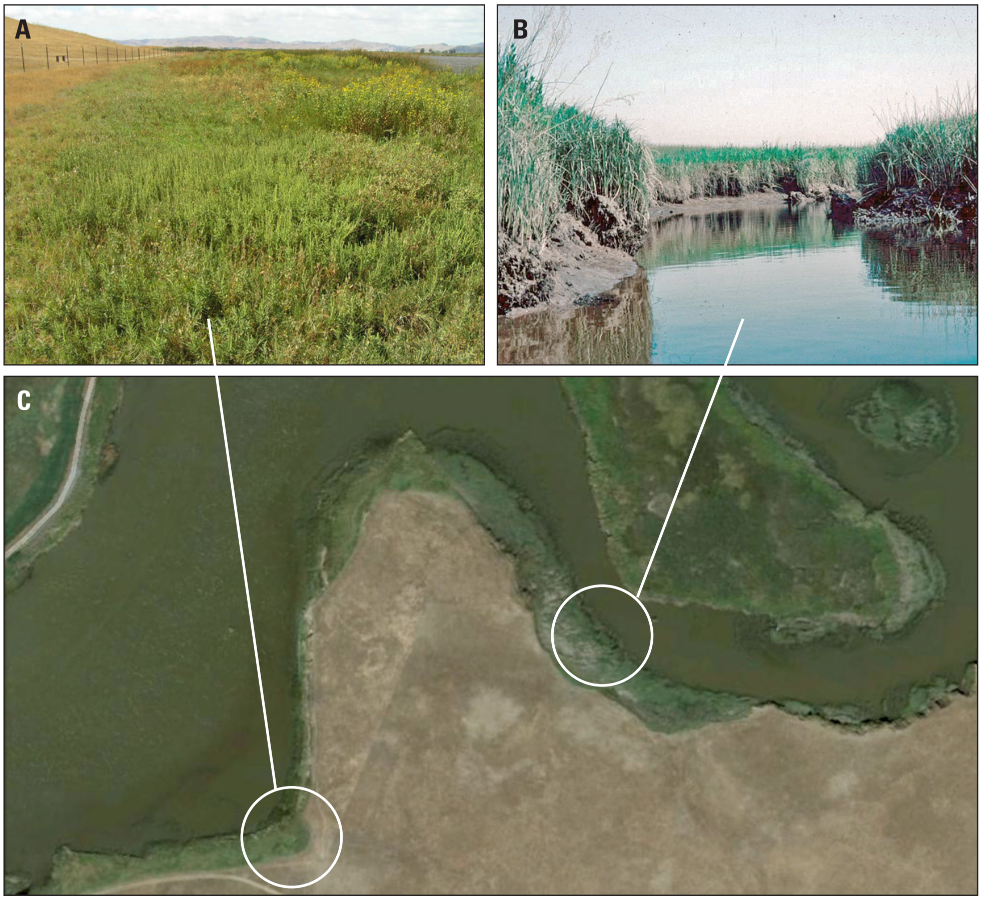


**Figure 6** Fringing high marsh and terrestrial ecotone at Rush Landing, Suisun Slough (A,C). Fringing low marsh along Hill Slough channel (B). Shown here are diverse patches of clonal forbs and graminoids dominating the high marsh plain, including *Juncus arcticus* ssp. *balticus* (Baltic rush), *Potentilla anserina* subsp. *pacifica* (silverweed), *Grindelia stricta* (gumplant), and *Euthamia occidentalis* (western goldenrod), while terrestrial ecotone shifts toward dominance by clonal perennials *Distichlis spicata* (saltgrass), *Leymus triticoides* (creeping wild rye) and *Ambrosia psilostachya* (western ragweed), and fringing low marsh at channel's edge is dominated by tall bulrushes, *Schoenoplectus californicus* and *S. acutus*.

*ciformis* (tufted hair-grass), *Juncus arcticus* subsp. *balticus* (Baltic rush) and other associated sub-shrubs and forbs. In addition to these broadly distributed species, the high fringing marsh supports species with small habitat ranges and narrow salinity tolerances, including *Sium suave* (water parsnip), the rare *Cicuta maculata* var. *bolanderi* (Bolander's water-hemlock), *Helenium puberulum* (sneezeweed), *Eryngium heterophyllum* (coyote-thistle), *Oenanthe sarmentosa* (water parsley) as well as more widespred perennial brackish wetland forbs such as *Euthamia occidentalis* (western goldenrod), *Ambrosia psilostachya* (western ragweed), and *Pluchea odorata* (marsh fleabane). Slumps and scarps of wave-impacted fringing marsh locally support opportunistic colonizers *Lilaeopsis masonii* (Mason's lilaeopsis, western grasswort) and *Isolepis cernua* (low club-rush). Below freshwater seeps in wave-cut low bluffs, fringing marsh at Rush Landing supports distinctive stands of freshwater marsh species discussed in the "Freshwater Seepage Landform" section. In recent years, *L. latifolium* has invaded fringing marsh at Rush Ranch, but at present is infrequent in this geomorphic setting.

## TIDAL MARSH PLAINS

Typically, tidal marsh plains (platforms) at Rush Ranch are wide tidal landforms dissected by complex, sinuous dendritic channels. Compared to surrounding, diked areas in Suisun Marsh, Rush Ranch channels have been altered significantly less. However, regional and on-site ditching, partial diking, and dam constructions have reduced sediment supply and thus altered the historic channel sinuosity. Internal landforms and vegetation zones of the tidal marsh plain (tidal creek banks and natural levees, artificial channels and dikes, tidally vs. poorly drained marsh plains, ponds, and turf pans) will be discussed individually.

## Tidal Creek Banks and Natural Levees

Tidal creeks are a key feature of natural estuarine wetlands that dissect marsh plains, and range from large creeks that rarely drain to small creeks that are covered with vegetation (Leopold and others 1993). The banks of these creeks are a distinct landform at Rush Ranch, formed by gradual overbank accretion of sediment and debris at stable bank positions. The vegetation present on these banks and levees is strongly influenced by subsurface drainage of the adjacent creeks (Figure 5). The tidal creek banks are regularly subjected to brackish tide water, and support tall emergent graminoids and forbs such as *Schoenoplectus* spp., *Carex* spp., and *Typha* spp. (cattails), as well as more diminutive plants such as *Lilaeopsis masonii*, *Isolepis cernua*, *Hydrocotyle verticillata* (water pennywort), and *Triglochin striata* (three-ribbed arrowgrass). Hill Slough's low creek banks support extensive colonies of *Carex lyngbyei* (Lyngbye's sedge), an oligohaline tidal marsh species typical of the Pacific Northwest (Figure 5D). This is a disjunct population apparently unique in the San Francisco Estuary. At Rush Ranch, it is established at the lower end of the low tule marsh zone.

The more elevated upper creek banks are often a habitat for tall forbs and subshrubs, such as *Grindelia stricta*, that provide dense flood refuge and cover for marsh wildlife. Upper creek banks also support rare or endangered plants, such as *C. h.* var. *hydrophilum*, *C. m. bolanderi*, and *Lathyrus jepsonii* subsp. *jepsonii* (Jepson's Delta tule pea). Invasive non-native clonal forbs such as *L. latifolium* also occupy this habitat. At Rush Ranch, the spread of *L. latifolium* is frequently along these tidal channels (Figure 7) and the upland margin of other tidal marshes near Potrero Hills (Grossinger and others 1998; Boyer and Burdick 2010).

In fresh to brackish tidal areas, small *Lilaeopsis masonii* and *Triglochin striata* are found in the marsh ground layer below the canopy of tall emergent macrophytes along tidal sloughs and slumping banks of in-channel islands. The macrophytes may include *S. californicus*, *S. acutus*, *Typha domingensis*, *T. angustifolia*, *T. latifolia*, and *Phragmites australis*, either in mixed or in monospecific stands. Extensive marsh plains within the brackish marsh are dominated by *Distichlis spicata*. Where tidal creeks introduce complexity, we also find *S. pacifica*, *Limonium californicum* (California sea-lavender) *Atriplex prostrata* (common spearscale), *G. maritima*, *Jaumea carnosa* (fleshy jaumea), *Triglochin maritima* (seaside arrowgrass), *Isolepis cernua* (club rush), *I. carinata* (keeled sedge), *Helenium bigelovii*, *P. odorata*, *D. cespitosa*, and *Oenanthe sarmentosa*. Rarer plants, such as *Symphyotrichum lentum* (Suisun Marsh aster), *L. j.* subsp. *jepsonii*, *C. m. bolanderi*, and *Eleocharis parvula* (dwarf spikerush) also occur in this zone. When the depth and duration of flooding increases during wet years, mid-zone diversity is reduced in Suisun Marsh as mosaics of more flood-tolerant *J. a.* subsp. *balticus* and *S. americanus* expand (Brenda Grewell, unpublished data).

## Artificial Channels and Dikes

The creation of channels and dikes at Rush Ranch most likely began in the late 19th century for agricultural purposes. Ditching of tidal marsh plains with poor drainage (mosquito ditches) or tidal marsh pans and ponds, such as in the "Mallard Slough" vicinity, created ponded habitats attractive to dabbling ducks (Wetlands and Water Resources, Inc. 2011). At Rush Ranch, non-engineered ditching extended and connected the distal ends of small tidal creeks. In addition, slough dams and partial dikes were constructed along the marsh perimeters on branches of Second Mallard Slough, Suisun Slough, and Hill Slough. The resultant steeply elevated berms line rectilinear channels, creating crests above the marsh plain that are only flooded at the most extreme high tides. Throughout most of Suisun Marsh, dikes (artificial levees) adjacent to tidal marshes have replaced much of the natural flood-refuge habitats formerly provided by natural marsh levees or terrestrial vegetation. In this artificial and constantly changing ecotone, ruderal species, such as the following, thrive: *L. latifolium, Annagallis arvensis* (pimpernel), *Brassica* spp. (wild mustard), *Raphanus* spp. (wild radish), *Foeniculum vulgare* (fennel), *Helminthotheca*


**Figure 7** Marsh view of the Upper First Mallard Branch during early phase (1995) of exponential spread of *Lepidium latifolium* (A and B) and dense infestation 15 years following (2007) initial colonization (C).

*echioides* (bristly ox tongue), *Conium maculatum* (poison hemlock), and *Rubus armeniacus* (Himalayan blackberry). These ruderal species are characterized by high reproductive abilities, fast growth rates, and short life-spans, and are thus capable of thriving on a frequently changing depositional area (Grime 1977).

## Tidally Drained Marsh Plain

This tidal marsh zone is influenced by surface and subsurface drainage of adjacent creeks and ditches, which limits soil waterlogging, salt accumulation from evapotranspiration, and ponding—in contrast to poorly drained marsh plains (discussed below). The tidally-drained marsh plain at Rush Ranch is extensive, as compared to other relict tidal marsh-

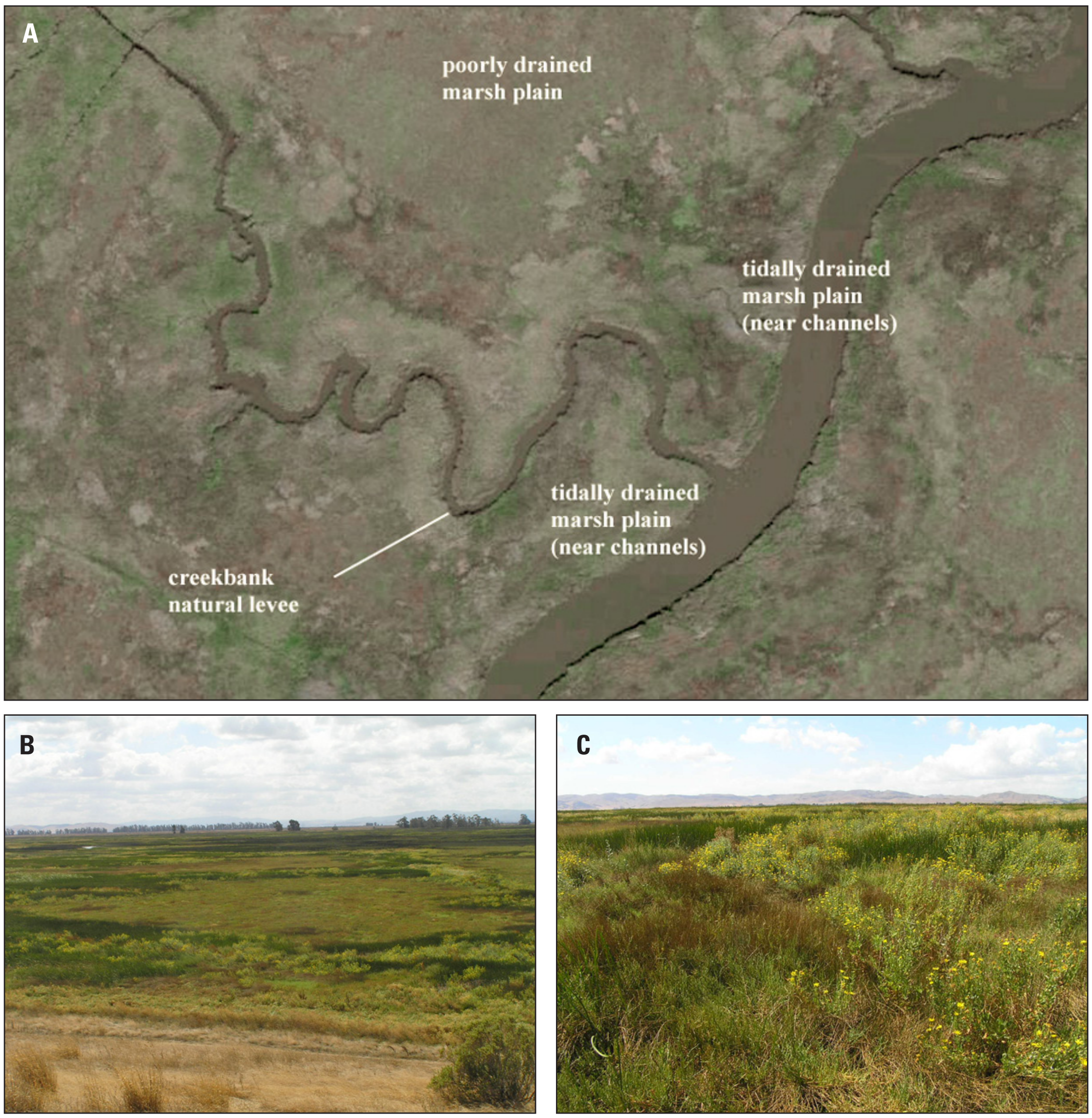


**Figure 8** The high marsh plain (marsh platform) of Rush Ranch, shown above in aerial, oblique, and ground views (A–C), is a complex and highly dynamic mosaic of vegetation patches. Tidally drained marsh plains near channels (B) support diverse assemblages of both tall and low-growing forbs, rushes, and bulrushes—and also massive infestations of *Lepidium latifolium* (perennial pepperweed). Poorly drained marsh in the interior portions of the plain (C), remote from channels, supports three-square bulrush, saltgrass, Baltic rush, gumplant, and pickleweed assemblages.

es with small to no remnant tidal plain habitats (Figure 8A, 8B). This brackish landform at Rush Ranch is dominated by mixed creeping subshrub and graminoid species, such as *D. spicata*, *S. pacifica*, and *L. latifolium*. Plants, such as *G. maritima* and *Senecio hydrophilus* previously common in this zone throughout the estuary, persist at Rush Ranch, yet rarely occur on other similar properties. Within the well-drained marsh plain, there are middle- and high-elevation areas (high and mid marsh) occurring in a patchy mosaic distribution indicative of altered hydrology.

Traditionally, high marsh is defined as the area from approximately mean higher high water (MHHW) to extreme high water (occurring with spring tidal cycles) (Josselyn 1983; Peinado and others 1994). Much of the marsh native plant and animal biodiversity, including regionally rare and endangered species, is found, in particular, in the high marsh. The common holoparasitic vine, *Cuscuta pacifica* var. *pacifica* (salt marsh dodder), and the endangered root hemiparasite, *C. m.* subsp. *molle*, suppress perennial dominants in the community and enhance plant species richness in the high marsh (Grewell 2008a, 2008b). The marsh at Rush Ranch is primarily high marsh plain dominated by *D. spicata*, *S. pacifica*, *F. salina* and, with locally abundant *C. p.* var. *pacifica* and *G. s.* var. *angustifolia* or *G. × paludosa*. At Rush Ranch, *Arthrocnemum subterminale* (Parish's glasswort) is found in upper Spring Branch Creek, the emphemeral drainage in Suisun Hill Hollow below Suisun Hill spring, the stock pond and Grizzly Island Road, and as small rare patches near the terminus of first-order tidal creeks associated with Second Mallard Branch Slough. Other co-occurring species include introduced *Cotula coronopifolia* (brass buttons) in areas where water occasionally pools, and *A. prostrata*. Endangered *C. m.* subsp. *molle* (Figures 3 and 5) also occurs along high marsh ecotones, drainage divides within marsh plains, and near high order tidal creeks. Similar to levee and berm habitats, the high marsh is also susceptible to invasion by many non-natives including *L. latifolium*, *Apium graveolens*, *Lotus corniculatus* (bird's foot trefoil), *Bromus diandrus* (ripgut brome), *H. cylindrica*, *P. incurva*, and *P. monspeliensis*. *Rumex crispus* and *R. pulcher* (curly and fiddle docks) have been reported at the edges of brackish high marshes at Rush Ranch, but are not believed to be invasive (Baye and others 2000).

In slight depressional areas of the marsh plain that experience more extended hydroperiods, a number of marsh plants co-occur in a patchy mosaic distribution that reflects subtle changes in sediment characteristics and hydrology. Plant species here include *J. carnosa*, *F. salina*, *C. p.* var. *pacifica*, *Triglochin maritima*, *D. spicata*, *J. a.* subsp. *balticus*, and *S. pacifica*. *Glycyrrhiza lepidota* (wild licorice), rare in tidal wetlands, is associated with *J. a.* subsp. *balticus* in the marsh plain adjacent to Hill Slough. In this zone, *S. pacifica* is often in its tallest, most robust form among all habitats within the marsh (SEW 1996). Although Watson and Byrne (2009) found that *D. spicata* had been nearly replaced by *S. americanus* and *B. maritimus* in the mesohaline marshes, including Rush Ranch, their sampling was limited to a single season. Historically and in modern times, *D. spicata* is the main dominant in this zone, also reaching its maximum height form in this habitat (Mason 1972). Well-drained peat sediments bordering first order tidal creeks and mosquito ditches dissect the plain and support the endemic, federally endangered Suisun thistle (Figure 9, *C. h.* var. *hydrophilum*) (Fiedler and Keever 2003; Fiedler and others 2007), as well as *S. hydrophilus*, *P. odorata*, and *Grindelia* spp. The five most dominant plant species (measured as canopy cover) associated with the endangered *C. h.* var. *hydrophilum* which borders tidal creeks have been native *P. a.* var. *pacifica*, *S. americanus*, *J. a.* subsp. *balticus*, and *G. stricta*; and exotic *L. latifolium* (Fiedler and others 2003). In addition to these dominant species, results of a marshwide census at Rush Ranch indicate exotic *A. graveolens*, *A. prostrata*, and *R. crispus* also frequently occur with the endangered thistle though they are not dominant in the association (Fiedler and others 2003). It is interesting to note that the dominant plant species associated with endangered *C. h.* var. *hydrophilum* are also recognized to be key indicator species for California black rail breeding habitat (particularly *S. americanus*) and California clapper rail breeding habitat (particularly *G. stricta*) in Suisun Bay and North Bay marshes (Evens and Nur 2002; Evens 2010).

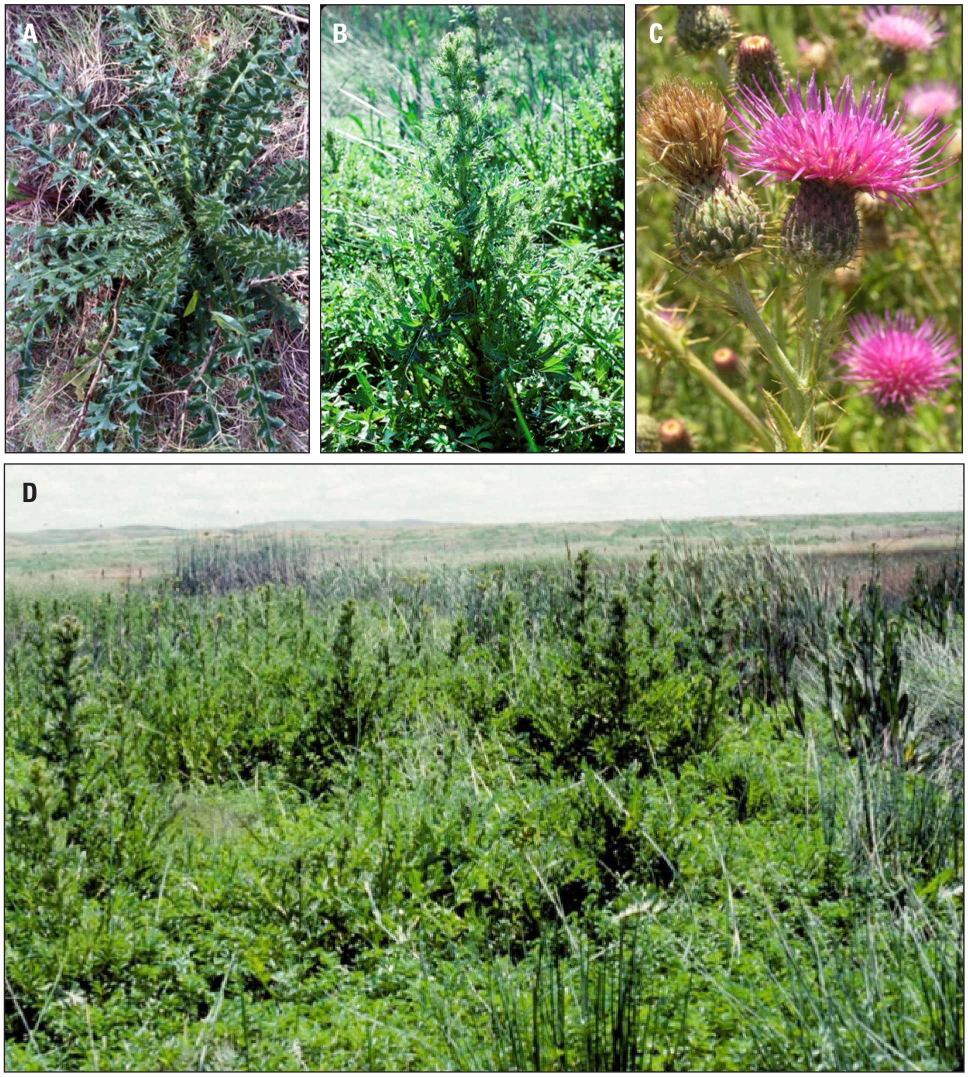


**Figure 9** Rush Ranch supports the last core population of the endangered *Cirsium hydrophilum* var. *hydrophilum*, (Suisun thistle), formerly a widespread and abundant endemic species of Suisun Marsh (A, basal rosette, B, bolting shoot, and C, flower). Before the invasive spread of *Lepidium latifolium* at Rush Ranch, the rare thistle was part of a diverse emergent macrophyte community (D) occurring frequently with *Schoenoplectus americanus*, *Potentilla anserina* subsp. *pacifica*, and *Senecio hydrophilus* along first order tidal creeks (1992 photo, first-order tidal creek, first Mallard Branch drainage, Rush Ranch).

## Poorly Drained Marsh Plain

Contrasting with tidally drained marsh plain, the poorly drained marsh plain habitat is remote from tidal channel drainage, and is inefficiently drained, primarily by slow overland sheeting flow or very slow infiltration and evapotranspiration. Elevated groundwater and soil salt accumulation from evapotranspiration are important structuring processes in this marsh plain zone. Similar to the well-drained marsh habitats, this habitat is dominated by mixed creeping subshrub and graminoid species, such as *D. spicata*, *S. pacifica*, and recently, *L. latifolium*. At Rush Ranch, patchy sections of non-native *P. australis* occur in the poorly drained portions of the marsh plain habitats. Of all the zones on the well-drained marsh plain, the *D. spicata*-dominated zone is least invaded by *L. latifolium*, potentially from its poor drainage and the long hydroperiod that results (Christine Whitcraft, unpublished data).

## Marsh Plain Ponds

The ecogeomorphic origins of tidal marsh plain ponds (variously termed pools, ponds, pans, or pannes in different regions and times (Harshberger 1916; Pethick 1974; Adamowics and Roman 2005) in Suisun Marsh are not known, but may have structure and secondary origins similar to those in mature high-peat tidal marshes of the northeast U.S. (Wilson and others 2009, 2010). These ponded depressions in the tidal marsh plain are isolated from drainage networks, allowing them to maintain permanent standing water, except where they have been degraded or destroyed by marsh ditching (MacDonald and others 2010). As a rare vegetation habitat at Rush Ranch, the ponds support *S. pectinata* and epiphytic green algae. The tidally restricted ponds of Goat Island Marsh (diked marsh) also support stands of *S. pectinata* and the floating leaves of *Potamogeton nodosus* (pondweed).

### High-Marsh Pans (Turf Pans)

These high-marsh pans occur on the upper edges of the high marsh to the lower edges of the alluvial fan. They are often poorly drained during high winter tides and dry in the summer neap tides. The vegetation on these pans is dominated by turf-like low or prostrate perennial and annual graminoids, forbs, and subshrub vegetation. They are similar in structure to playas (shallow-flooded, seasonally desiccated, and hypersaline wetlands in arid or semi-arid flats or basins) or saline vernal pools, and dominated by annual forbs, graminoids, perennial grasses, and prostrate subshrubs. These species include *P. monspeliensis*, *H. cylindrica*, *Lasthenia glabrata* subsp. *glabrata* (goldfields), and *Juncus bufonius* (toad rush). Plants such as *Triphysaria versicolor* subsp. *versicolor* (butter and eggs) appear rarely in the turf pans of south Rush Ranch tidal marsh in association with *L. g.* subsp. *glabrata*, *I. cernua*, and *J. bufonius*, or prostrate *S. pacifica*. This is ecologically distinctive as the only reported occurrence of *T. versicolor* subsp. *versicolor* in a brackish tidal marsh; the species is typically found in the region within seasonal wetlands and alkali grasslands. *L. latifolium* appears to be consistently excluded from the summer-desiccated high turf pans, potentially by high-porewater salinity or low porewater in general.

In contrast to many estuarine marshes, the high intertidal zone of San Francisco Estuary brackish wetlands can support the greatest richness of plant species in the marsh. However, at limited locations in the Suisun Marsh, where the highest marsh elevation zone is still intact, tides are muted, summer temperatures can exceed 38 °C, soil porewater can be hypersaline (>40 ppt, and in places >100 ppt) (Grewell and others 2007; Grewell 2008a), and only *A. subterminale*, *S. pacifica*, and *Cressa truxillensis* (alkali weed) are found.

## FRESHWATER SEEPAGE SITES

Unique communities can occur on the upper edge of brackish marshes, where saltwater rarely reaches, or where salt is diluted by freshwater seepage. *Oenanthe sarmentosa* can be relatively abundant in wet years, particularly in or near freshwater seepages adjacent to low shoreline bluff scarps or drainages from upland swales. Other predominantly freshwater marsh species, including *Mimulus guttatus* (monkeyflower) and small-fruited sedge, appear anomalously in the middle marsh zone of fringing marshes at Rush Landing, below seeps in the high marsh zone that support *Sisyrinchium bellum* (blue-eyed grass) and mixed stands of *C. barbarae* and *Leymus triticoides* (creeping wild rye).

## SEASONAL WETLANDS

The primary seasonal wetland at Rush Ranch occurs along the Spring Branch corridor between the South Pasture Trail and Grizzly Island Road. Before 19th century alterations, this area was an extension of the historic Holocene tidal wetland. The freshwater input at this site is inhibited by a stockpond and the road upstream of the site; in addition, the tidal flow within this area is restricted by a berm and by a culvert (pipe) under the trail at the west end of the area. Despite these flow restrictions, this area retains some plant species typical of a seasonal wetland habitat. This habitat is dominated by non-native grasses: *Hordeum marinum* subsp. *gussoneanum* (Mediterranean barley), *Lolium multiflorum* (Italian ryegrass), *P. monspeliensis*, *H. cylindrica,* and *P. incurva*. However, there is muted tidal influence from First Mallard Branch Slough, and in wetter years, the soil is inundated and saline as indicated by the presence of obligate wetland plants: *A. subterminale*, *S. pacifica*, *C. truxillensis*, *F. salina*, *J. arcticus*, and *B. maritimus*. These plant species persist within this habitat, occupying remnant channels and floodplain. Ephemeral vernal flora along the terrestrial ecotone at Upper Spring Branch also includes *Lepidium* *oxycarpum* (forked pepperweed), *Muilla maritima* (common muilla), *Lasthenia glabrata* subsp. *glabrata*, *Tyiphysaria eriantha* subsp. *eriantha*, *T. versicolor* subsp. *faucibarbata*, and in some years, the rare *Lasthenia conjugens* (Contra Costa goldfields).

## DIKED MARSH

Fringing marshes throughout the Suisun Marsh were frequently converted to diked marshes for hunting. At Rush Ranch, before 1900, the Rush family added a muted-tidal impoundment of tidal marsh (the diked marsh south of Goat Island) and a hunter's cabin, and partial diking within the marsh plain also supported hunting pursuits on site. Today, the impoundment includes a more complete, but low levee along Suisun Slough; two water-control structures (at the north and south ends) allow limited inundation from the neighboring slough. Although the dikes and water-control structures at Rush Ranch have not been thoroughly maintained, water levels within the diked marsh do not fluctuate to the full extent of the surrounding un-diked marsh. There is no levee on the eastern–landward side of the diked marsh. Here, tall, robust stands of *S. pacifica* and *D. spicata* transition to grassland.

While diked, non-tidal marshes share some of the dominant plant species with natural marsh areas, their altered hydrological conditions do not support many of the rare or uncommon plant and animal species found in the more natural tidal marshes. Such is the case at Rush Ranch. The diked marsh supports dense stands of native cattails (*Typha latifolia*, *T. domingensis*) and bulrushes (*Schoenoplectus californica*, *S. acutus* var. *occidentalis*, *S. pungens*, and *S. americanus*). In addition, *P. australis* has colonized the more disturbed areas along the south edge, with observed spread into the more interior regions.

The artificial levee around the diked marsh supports an abrupt break in vegetation across a short and artificially steep slope, bordering a narrow fringing marsh. However, there are narrow bands of middle and high brackish marsh vegetation on the levee, including *D. spicata*, *S. pacifica*, and *G. s.* var. *augustifolia*, as well as *Euthamia occidentalis* (western goldenrod) and *Calystegia sepium* (morning-glory). The upper zones of dikes are typically weedy, and support a variety of introduced and invasive species, including *Rubus armeniacus* that frequently weakens the structure of the levee itself. The dike at the Goat Island Marsh at Rush Ranch is no exception, and contains a community dominated by *R. armenaicus*; annual forbs; and non-native forbs, including *L. latifolium* in small patches, *Raphanus sativus* (cultivated radish); as well as large colonies of *P. australis* that extend from the adjacent slough and diked marsh. Potential plans to restore tidal inundation to this area would dramatically alter the existing vegetation patterns.

## TIDAL MARSH—TERRESTRIAL ECOTONES

### Lowland Grassland (Sedge Rush Meadow)

Since grazing began to be restricted at Rush Ranch in the 1990s, the lowlands (sandy to silty alluvial fan edges near sea level) have regenerated extensive stands of a dominant native clonal perennial grass, *L. triticoides*, along the ecotone between alluvial fan edges and tidal marsh. *L. triticoides* forms extensive, spreading clonal colonies that coalesce and extend up to the fence-line that restricts grazing (currently less than 10 to 20 m above the highest tide lines). This grass also extends down to intergrading stands of *S. pacifica*, *D. spicata*, *C. truxillensis* and *F. salina*. *Leymus triticoides* is abundant to dominant in floodplain grasslands and lowland swales, and was a likely dominant element of lowland mesic or seasonal wetland grasslands in California (Holstein 2001). Its recent spread in areas where grazing pressure has been reduced at Rush Ranch and elsewhere where agricultural crop production was abandoned, suggests that it was a widespread, if not dominant, element of tidal marsh ecotones with lowland grasslands. From our perspective, the stands of *L. triticoides* at Rush Ranch may represent the most extensive and phenotypically diverse of any remnant tidal marshes in Suisun Marsh and the greater San Francisco Estuary.

After intensive cattle grazing was locally restricted, other clonal, graminoid species of seasonal wetland sedge meadows and grasslands have regenerated extensive, locally dominant stands at the tidal marsh ecotone of Rush Ranch, including *Carex* *praegracilis* (field sedge; locally abundant at southeastern Rush Ranch tidal marsh edges), and *Carex barbarae*, particularly near seeps or swales with seasonally saturated or mesic soils.

### Riparian Bluffs

The north–aspect bluffs (wave-cut or channel-cut scarps in low sandstone hillslopes) of Suisun Slough and Hill Slough support remnants of native woody riparian scrub that are otherwise very scarce in swales of Rush Ranch and Potrero Hills, which are heavily grazed. The steep bluffs are inaccessible to cattle, and likely have provided a natural refuge from grazing where slopes approach vertical and support shallow seeps. The ground layer of the riparian bluffs includes lowland grassland–sedge meadow elements (*L. triticoides*, *C. barbarae*); the patchy woody shrub thickets are dominated locally by *Rosa californica* (California rose), *Sambucus mexicana* (elderberry), *Toxicodendron diversilobum* (poison oak), and *Baccharis pilularis* (coyote brush). The lower branches of riparian scrub in some locations provide structural support for vines of the rare *L. j.* var. *jepsonii* established in the upper tidal marsh edge below the bluffs. Large patches of *R. armeniacus* also occur in the riparian bluffs of Hill Slough.

### Active Alluvial Flats

The "hollows" of Suisun Hill and Spring Branch Creek (shallow ephemeral creeks and the swales that drain grasslands) develop low-gradient lower reaches that form braided alluvial fan distributaries with disturbed, fine, slightly saline sands and silts (derived from marine sandstones), which grade into tidal marsh edges. The alluvial flats are, for the most part, intensively grazed and trampled, and include barrens as well as herbaceous lowland grassland assemblages similar to those of tidal marsh ecotones, including *Lolium perenne* (ryegrass), *D. spicata*, *F. salina*, and *C. truxillensis*. Near low-channel scarps and relatively well-drained edges, stands of *Hemizonia fitchii* (spikeweed) and *A. subterminale* are locally common.

## MODERN TRANSFORMATIONS

### Climate Change

It is particularly noteworthy that the estuary's regional climate in the historic period (post-1850) has been relatively stable compared with the majority of the tidal marsh stratigraphic record, with most of the historic change in the salinity signal resulting from water diversion in the Delta (Byrne and others 2001). The primarily fresh–brackish phase of Rush Ranch tidal marshes known from the early historic period is not a permanent or prevailing condition, but a long freshwater phase that began only 750 yr BP. Most significantly, perhaps, is that the entire geomorphic and ecological history of Rush Ranch tidal marsh plains occurred under a regime of slow sea level rise and gradual accretion of marsh peat (1.3 mm $yr^{-1}$) during the formation of the mature marsh plain (Byrne and others 2001). No part of the marsh's history reflects the conditions that are expected in the 21st century: accelerated sea level rise rates significantly greater than 2 mm $yr^{-1}$ and a prolonged warmer climate with reduced Delta outflows, and seasonal Delta outflow limited to the wet season because of reduced or absent of Sierra snowpack. Modern operation of state and federal water projects reduce seasonal and annual outflow and salinity variability, yet climate change is the most powerful driver of long-term variability at Rush Ranch, and regionally (Enright and Culberson 2009).

Over the past 30 years, the large annual ranges of channel salinity in Suisun Marsh have also had considerable temporal and spatial variation. This high inter-annual variability in salinity is likely key to a productive ecosystem that supports native biota (Atwater and others 1979; Fox and others 1991; Peterson and others 1995; Byrne and others 2001; Malamud–Roam and others 2007; Moyle and others 2010). Summer salinity is projected to increase in the Suisun Marsh because increasing spring air temperature is causing snowmelt runoff into the estuary to occur earlier in the year (Knowles and Cayan 2002).

Recent projections of areas vulnerable to sea level rise suggest variable effects at Rush Ranch that correspond to the magnitude of increases in water elevation (Knowles 2010). For example, with sea level increases of 50 to 150 cm relative to MLLW, it is projected, based on present day elevations, that wetland elevations of the diked wetland and Hill Slough regions of Rush Ranch will drop to below MLLW tidal datum, while the tidal marsh associated with Suisun and Cutoff Slough remains above MLLW. Projections of wetland elevation increases in the range of 100 to 150 cm above MLLW suggest Rush Ranch tidal wetlands will be among extremely rare and isolated wetlands above MLLW, relative to a largely inundated Suisun Marsh. However, these projections ignore the potential for vertical accretion and lateral migration of wetlands (Knowles 2010). Certainly, understanding how Rush Ranch vegetation may respond to predicted sea level rise will depend on understanding sediment supply and accretion (Orr and others 2003; Callaway and others 2007). At Rush Ranch, the average marsh accretion rate over the last 750 years has been approximately 1.5 mm $yr^{-1}$, close to the average rate of sea level rise at San Francisco for the period AD 1855–1986 (Lyles and others 1988; Byrne and others 2001). The actual changes in salinity and inundation regimes at sites such as Rush Ranch are difficult to predict, and heterogeneous effects could result in increased plant species evenness (Watson and Byrne 2009). Some studies suggest that increases in salinity and submergence of wetlands associated with sea level rise in Suisun Marsh will prompt local-scale declines in plant species richness and productivity (Callaway and others 2007). If Rush Ranch tidal marsh plain accretion rates fall below rates of accelerated sea-level rise, and hydroperiods increase, large-scale marsh vegetation zonation changes and dominance shifts within both the marsh plain and terrestrial ecotone would be expected (Watson and Byrne 2009). High marsh and terrestrial ecotone assemblages would be likely to shift landward and invade low-gradient stream valleys such as Spring Branch Creek and Suisun Hill Hollow. Expansion of lower tidal marsh assemblages tolerant of prolonged flooding, such as tules, bulrushes, or sedges, would be expected to displace saltgrass, rush, and perennial forb assemblages within the tidal marsh platform. High marsh assemblages dominated by tall perennial forbs along tidal creek banks, internal to the marsh plain, would also be at risk of conversion to more flood-tolerant wetland graminoid assemblages.

Failed levees and expanded subtidal basins in the vicinity of Suisun and Montezuma sloughs can result in a reduction of tidal range due to tidal prism increase. If such tidal damping interactions with sea level rise are significant at Rush Ranch, dominance by flood-tolerant wetland graminoid vegetation may be intensified. This condition may have parallels with the earliest vegetation history of Rush Ranch, evident in sediment cores that show foundering *Cyperaceae* and *Poaceae*-dominated marsh and mudflat in its early stages of formation prior to 1750 cal yr BP, before the high marsh platform formed (Byrne and others 2001).

## Future Research Needs

Assembling information about the vegetation history and current status at Rush Ranch highlights gaps in our knowledge. The SF Bay NERR has identified these research gaps as a management priority in the 2011–2016 Management Plan to provide ideas for researchers, especially graduate students, as well as to facilitate cooperation among researchers. We see one major area of focus as determining the types and levels of ecological effects that result from the SLT's different management actions (i.e., grazing, fencing locations, and stockpond management) that could affect estuarine vegetation communities on a large geographic scale. In addition, development of standardized and regularly occurring monitoring of submerged aquatic vegetation communities and rare plant populations would improve the ability to manage for their success and continued recruitment. In parallel with monitoring rare plant populations, it would be ideal to conduct research to support predictive modeling of non-native plants within the property, and among neighboring properties. Successful modeling of potential ranges of a given plant species requires growth parameters for each invasive plant through controlled field or greenhouse experiments. Several ecological restoration projects are being considered for Rush Ranch while surrounding tidal wetlands are heavily invaded with exotic plant species. Given the many exotic species in the estuarine flora at Rush Ranch, research is needed to support ecologically-based, comprehensive (multiple species) weed-management strategies that will promote recovery of sustainable native plant communities. Restoration projects should be paired with research on short- and long-term responses by target weeds, native plant indicator species, and native plant communities to restoration and management actions. Research is needed to evaluate the range of variability in estuarine conditions (i.e. salinity, tidal flows) that will be needed to support more heterogeneous, native vegetation associated with specific hydrogeomorphic landform units (see Moyle and others 2010). Focusing on these data gaps can inform adaptive management planning and actions for conservation and recovery of native plant communities at Rush Ranch.

Climate is changing across a range of scales, from local to global, yet the ecological consequences of these predicted changes are difficult to understand and predict. Accurately predicting how climate change will affect plant diversity and distribution is critical to the development of conservation strategies and management plants. Incorporation of climate change factors, such as sea-level rise and subsidence, is essential to accurate predictions. Thus, one need is for manipulative experiments that address how life-history traits of species, or processes such as migration, might affect how well plant species respond to climate perturbations. In addition, climate change is also predicted to interact with other drivers of biodiversity change such as habitat destruction and fragmentation, or the introduction of non-natives.

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