Rooting and Foraging Effects of Wild Pigs on Tree Regeneration and Acorn Survival in California's Oak Woodland Ecosystems[1]

Rick A. Sweitzer[2] and Dirk H. Van Vuren[3]

Abstract

Wild pigs (*Sus scrofa*) have been widely distributed by humans and significant populations now occur in oak-dominated ecosystems in California. Because they are omnivorous and forage by rooting, wild pigs have the potential to impact a wide variety of plants and animals directly by consumption and indirectly through disturbance. In 1998, we initiated a long-term study of the ecological effects of wild pigs on oak woodland ecosystems in California using multiple exclosures with paired control plots targeting four oak communities in the north and central coast region of California that vary in population density of wild pigs. Soil disturbance by wild pigs was significantly higher in areas where wild pig densities are high. Rooting significantly reduced aboveground plant biomass in oak grassland and oak woodland habitats, and may therefore reduce forage availability for herbivores in areas with widespread rooting. Rooting disturbance may be significantly reducing survival of tree seedlings, thereby limiting tree regeneration in oak woodlands. Experimental plots associated with high masting oak trees indicated that wild pigs significantly reduced acorn survival and, therefore, reduced the availability of acorns for germination and consumption by native wildlife.

Introduction

Pigs (*Sus scrofa*) are a large ungulate native to Eurasia and North Africa, and are now widely distributed as feral animals in many areas including California (Oliver and Brisbin 1993). Wild pigs in California originated from domestic pigs foraging on acorns in oak woodlands around Spanish settlements in the late 1700s (Mayer and Brisbin 1991). They have expanded significantly in California in recent years related to a combination of hunting-related introductions, spread of agriculture, releases of domestic swine by hog farmers, and natural dispersal (Waithman and others 1999). Although wild pigs are popular among sport hunters, expanding populations increasingly conflict with agricultural and conservation activities by crop depredation and rooting disturbance in natural areas (Giusti 1993).

Previous studies of wild pigs in mainland California have provided information on aspects of the population ecology of wild pigs (Barrett 1978, Schauss and others 1990), but little quantitative information is available on the effects of wild pigs on the oak-dominated regions they occupy (Kotanen 1995). In 1998 we initiated a large-

[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.
[2] Assistant Professor, Department of Biology, University of North Dakota, Grand Forks, ND 58202 (e-mail: Richard_Sweitzer@und.nodak.edu)
[3] Professor, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616 (e-mail: dhvanvuren@ucdavis.edu)

scale study of the ecological effects of wild pigs in oak woodland ecosystems. Research began in May 1998 and will be continuing through October 2004. The primary objectives of the study are to assess the effects of rooting and foraging by wild pigs on (1) regeneration potential of oak trees, and (2) diversity and abundance of native and nonnative plants and terrestrial vertebrates (small mammals, reptiles and amphibians). In 1998 and 1999 we established multiple fenced exclosure and control plots at research sites in the central and north coast regions of California to begin to evaluate hypotheses about how rooting and other activities of wild pigs impinge on oak woodland ecosystems. A variety of activities is underway *(table 1)*; here we will focus on research assessing how rooting and foraging by wild pigs influences tree regeneration and forage availability for native wildlife.

Table 1—*Summary and description of different research activities being used to assess the effects of wild pig rooting and foraging activities on oak woodland ecosystems in California.*

Activity	Brief description	Target organisms/purpose
Rooting transects	100 m line transects with five 2 m^2 quadrats, one every 20 m	Plants - vegetative cover and biomass production
Oak canopy experiments	3x3 m fenced exclosures with four 1x1 m acorn monitoring plots nested within	Acorns - acorn survival rates and regeneration potential
Tree seedling transects	40x4 m line transects, some nested within fenced exclosures	Oaks, conifers, woody shrubs - regeneration
Mammal trapping	7x7 trap grids 7-8 m spacing, some grids enclosed by fenced exclosures	Small rodents - species list, species richness and diversity, relative abundance
Pitfall arrays	Y-shaped arrays composed of a central trap and three arms with three traps along each arm. Some arrays within fenced exclosures	Rodents, amphibians, reptiles, invertebrates - species lists, species richness and diversity, relative abundances
Timed searches	30 minute time-constrained searches for reptiles and amphibians	Reptiles, amphibians - species lists, species richness and diversity, relative abundances
Coverboards	transects along drainages each with 20 coverboards (0.6x0.6 m) spaced every 20 m	Amphibians, reptiles - species lists, species richness and diversity, relative abundances
Vegetation plots	2x2 m plots, some nested within fenced exclosures	Native, nonnative grasses - species lists, species richness and diversity, relative abundances

Study Areas

Introduced wild pigs may or may not negatively influence ecological processes operating in mainland ecosystems, except perhaps in areas with relatively high-density populations (Sweitzer 1998). Thus, research sites selected for this study were focused in several relatively small areas of the central and north coast regions of California where high-density wild pig populations are centered (delineated in Waithman and others 1999). Within these regions, study sites were further restricted to (1) areas without free-ranging livestock because cattle grazing may interfere with efforts to assess the effects of wild pigs, (2) areas where control activities provided opportunities for comparative research between a site with ongoing wild pig control and a nearby site without wild pig control, and (3) sites where we were allowed to construct small exclosures as part of experimental comparisons. In the north coast region of the state we established three research sites in summer 1998; Austin Creek State Recreation Area (Austin Creek SRA, western Sonoma County), Sugarloaf Ridge State Park (Sugarloaf Ridge SP, eastern Sonoma County), and the McCormick Sanctuary (eastern Sonoma County). In summer 1999 Henry Coe State Park (Henry Coe SP, Santa Clara County) in the central coast region of the state was added to the study. Austin Creek SRA and Henry Coe SP were experimental sites where different types of fenced exclosure plots were established to allow for direct experimental evaluation of pig effects. Sugarloaf Ridge SP was a site with long-term and ongoing wild pig control, and McCormick Sanctuary was a site with no organized wild pig control, located immediately to the north of Sugarloaf Ridge SP. Sugarloaf Ridge SP and McCormick Sanctuary were considered comparative research sites, with data collected at Sugarloaf Ridge SP compared to those from McCormick Sanctuary.

Methods

Habitat Plots and Exclosures

Several research activities were focused around habitat plots and/or exclosures established in oak grasslands, oak woodlands, mixed forests, and meadows. At each experimental research site we established four large 50x50 m fence exclosures designed to allow foraging access by all herbivores except wild pigs. Exclosures were built by wiring 0.9 m high field fence to 1.9 m fence posts driven into the ground every three meters. Rebar stakes secured fencing to the ground between posts. The low height of the field fence and large mesh openings (10x10 cm) allowed deer and small vertebrates to easily enter. For each exclosure, we also staked out a matched 50x50 m control plot, usually within 500 m of the exclosure. Nested within each 50x50 m exclosure and control habitat plot were (1) a 7x7 small mammal live trap grid, (2) six 4x40 m seedling belt transects, (3) a y-shaped pitfall trap array with 10 traps, and (4) several 2x2 m vegetation plots near each of the four corners. Details and data on small mammal trapping, pitfall trapping, and vegetation plot analyses will not presented in this paper due to space constraints.

Exclosures at Austin Creek SRA were located in four different habitats: oak grassland, oak woodland, mixed woodland, and riparian meadow. At Henry Coe SP two exclosures each were established in oak woodland and oak grassland habitats. At both Sugarloaf Ridge SP and McCormick Sanctuary, 50x50 m plots were staked out in four different types of habitat (oak grasslands, oak woodlands, mixed woodlands, and riparian meadows). Plots in each habitat at Sugarloaf Ridge SP and McCormick Sanctuary were carefully surveyed prior to establishment so as to match them ecologically and thereby allow for research comparisons.

Rooting Dynamics

We characterized the extent of wild pig rooting disturbance at all research sites using quadrat sampling along 100 m “rooting transects.” During the spring periods of 1999 and 2000, 14 to 20 100-meter rooting transects were surveyed at each research site within oak grassland and oak woodland habitats. For each 100-m line transect randomly situated within the appropriate habitat types, five 2.0 m^2 quadrats (PVC pipe frame) were randomly placed from 1 to 10 meters to the left or right side of the transect line at 20 meter intervals. For each quadrat we noted the presence or absence of rooting, and prepared scaled down line drawings of rooted areas when rooting was present. During 1999, two of five quadrats along each rooting transect were randomly selected for sampling of total biomass production by clipping all nonwoody vegetation to ground level. Because this approach resulted in relatively few biomass samples from quadrats that were rooted, we altered our biomass sampling protocol for summer 2000. During summer 2000 we estimated biomass productivity in relation to rooting by randomly selecting two of the five sampling intervals (20, 40, 60, 80, 100 meters) along each 100-m rooting transect for biomass sampling. At the two randomly selected intervals, we laid out a 10-m tape to the left or right and perpendicular to the 100-m rooting transect. We then placed the edge of a 2 m^2 quadrat at the point at which the tape first intersected wild pig rooting, prepared a scaled down line drawing of rooting in the quadrat, and sampled all aboveground biomass by clipping nonwoody vegetation to ground level. Next, we established a 2 m^2 control biomass quadrat in an unrooted area, as near as possible to the rooted biomass quadrat, and matched to the dominant vegetation in nonrooted areas of the rooted quadrat. This control biomass quadrat was also sampled for aboveground biomass. Clipped vegetation was dried to constant weight for determination of dry matter biomass. For data from 1999, analyses were by linear regression of log transformed dry matter biomass by the estimated proportion of rooting in biomass plots. Data from 2000 were analyzed by linear regression of arcsin transformed proportional differences in dry matter biomass between matched rooted and control biomass plots against percent rooting disturbance in the rooted biomass plots.

Regeneration Potential in Oak and Mixed Forest Woodlands

Rooting by wild pigs may reduce tree regeneration by damaging or uprooting young seedlings. We used three different approaches to assess this hypothesis: (1) comparisons of data on tree seedling sizes along multiple 4x40 m "belt transects" in oak woodland and mixed forest habitats at all research sites, (2) comparisons of data on tree seedling size and number along belt transects in 50x50 m exclosure and control habitat plots in oak woodland and mixed forest areas at experimental research sites, and (3) comparison of numbers and sizes of tree seedlings in 3x3 m oak canopy exclosure and control plots, also at experimental research sites.

Belt transects were initiated at selected starting positions within continuous tracts of oak or mixed woodland. From starting positions for each belt transect, we randomly selected an azimuth from 0 to 359 degrees N and laid out a 40 m line transect. All tree seedlings encountered within two meters of either side of the tape were identified and measured from ground level to the terminal bud. A moveable 2x4-m rope frame was used to facilitate sampling seedlings along the 40-m transect line. As part of analyses of seedling data, we calculated an index to regeneration potential, defined as the ratio of large seedlings (>200 mm) to total seedlings, for each belt transect. A low regeneration index suggests that relatively few tree seedlings survived to a relatively large size where they may be less prone to mortality by rooting. Data on arcsine transformed regeneration indices were evaluated by analysis of variance (ANOVA).

At Austin Creek SRA and Henry Coe SP, additional belt transects in paired 50x50 m exclosure and control habitat plots in oak woodland and mixed woodland areas (Austin Creek SRA only) were used to experimentally assess effects of wild pig rooting on tree regeneration. Within the habitat plots, we defined six 4x40-m belt transects situated between and parallel to the 7x7 small mammal trap grid lines. During summer 2001 all exclosure and control belt transects were surveyed for tree seedlings. Data on log transformed seedling sizes and average numbers of seedlings noted along belt transects in paired exclosure and control habitat plots were evaluated by ANOVA. As part of oak canopy exclosure experiments described below, we also counted and measured all tree seedlings located in each oak canopy exclosure and paired control plot at Austin Creek SRA and Henry Coe SP during spring 2000 and spring 2001. Data on sizes and numbers of seedlings collected from oak canopy experiment plots also were evaluated by ANOVA.

Oak Canopy Experiments

Acorn consumption by wild pigs may reduce resource availability for native wildlife, while simultaneously limiting oak regeneration by consumption of acorns that might otherwise germinate. We tested these hypotheses with exclosure experiments beneath canopies of high acorn mast producing oak trees at Austin Creek SRA in 1998 and 1999 and Henry Coe SP in 1999. The design of "oak canopy experiments" included (1) mid-summer surveys of oak woodlands for high acorn producing oak trees (Category four acorn producers, Graves 1980), (2) establishing small 3x3m exclosure and control plots beneath the canopies of selected oak trees, and (3) monitoring numbers of acorns present on two 1x1m monitoring plots within each exclosure and control plot from mid-September to mid-December. Sixteen high-masting oak trees were selected for oak canopy experiments at Austin Creek SRA in 1998 (14 *Quercus kelloggii,* two *Lithocarpus densiflorus*). In 1999 at Austin Creek SRA, 5 of the 15 oak trees from 1998 (three *Q. kelloggii*, two *L. densiflorus*) retained sufficient acorns to continue acorn monitoring, and an additional 10 high masting trees were identified and selected for experiments, including two *Q. kellogii*, five *Q. agrifolia*, two *Q. lobata*, and one *Q. garryana.* Fifteen high-mast-producing oak trees were selected for experiments at Henry Coe SP in 1999: seven *Q. douglasii*, three *Q. agrifolia*, four *Quercus lobata*, one *Q. garryana*).

At each selected oak tree, exclosure and control designations were randomly assigned to each of two 3x3-m plots marked out beneath portions of tree canopies with approximately similar numbers of acorns (estimated visually). Exclosures for the experimental plots were built using the same design features as habitat plot exclosures. Control canopy plots were delineated by a single 1.9-m fence post at each corner. Within each exclosure and control plot, two 1x1-m acorn survival monitoring plots were staked out using short lengths of metal rebar. Beginning in mid-September and continuing until mid-December, the numbers of acorns present on acorn survival plots were assessed every 2-3 weeks. During periodic acorn counts, we discriminated between acorns from previous years and current-year acorns, and between immature and mature current-year acorns. We also recorded evidence of acorn foraging by wild pigs and other wildlife.

Results

Rooting Disturbance

Sixty-eight and 81 rooting transects were used to estimate wild pig rooting disturbance in oak grassland and oak woodland habitats during 1999 and 2000, respectively. Based on presence or absence of rooting in 2 m^2 quadrats along rooting transects, rooting was more widely distributed at research sites with relatively high densities of wild pigs (Austin Creek SRA, Henry Coe SP) compared to sites with low densities of wild pigs (Sugarloaf Ridge SP, McCormick Sanctuary). In 1999 the proportions of 2 m^2 quadrats with rooting along transects in all habitats ranged from 10 percent at Sugarloaf Ridge SP to 79 percent at Henry Coe SP ($\alpha<0.001$). Similarly, in 2000 the proportions of 2 m^2 quadrats rooted along transects in all habitats ranged from 13 percent at Sugarloaf Ridge SP to 92 percent at Henry Coe SP ($\alpha<0.001$). Analyses of line drawings of rooting disturbance in 2 m^2 quadrats in oak grasslands suggested that area rooted by wild pigs in 1999 was much lower at Sugarloaf Ridge SP compared to the other research sites (*fig. 1*; $\alpha<0.001$). In oak grassland habitats in 2000, however, less area was rooted at Sugarloaf Ridge SP and McCormick Sanctuary compared to Austin Creek SRA and Henry Coe SP (*fig. 1*; $\alpha<0.001$). There was less rooting in oak woodland habitats in 1999 at Sugarloaf Ridge SP and McCormick Sanctuary compared to both Austin Creek SRA and Henry Coe SP (*fig. 1*; $\alpha<0.001$). Also, rooting in oak woodland habitats in 1999 at Austin Creek SRA was higher than at Henry Coe SP *(fig. 1)*. In 2000 there was less rooting in oak woodland habitats at Sugarloaf Ridge SP and McCormick Sanctuary than at Austin Creek SRA and Henry Coe SP (*fig. 1*; $\alpha<0.001$). Also, in 2000 more area was rooted in oak woodlands at Henry Coe SP than at Austin Creek SRA *(fig. 1)*.

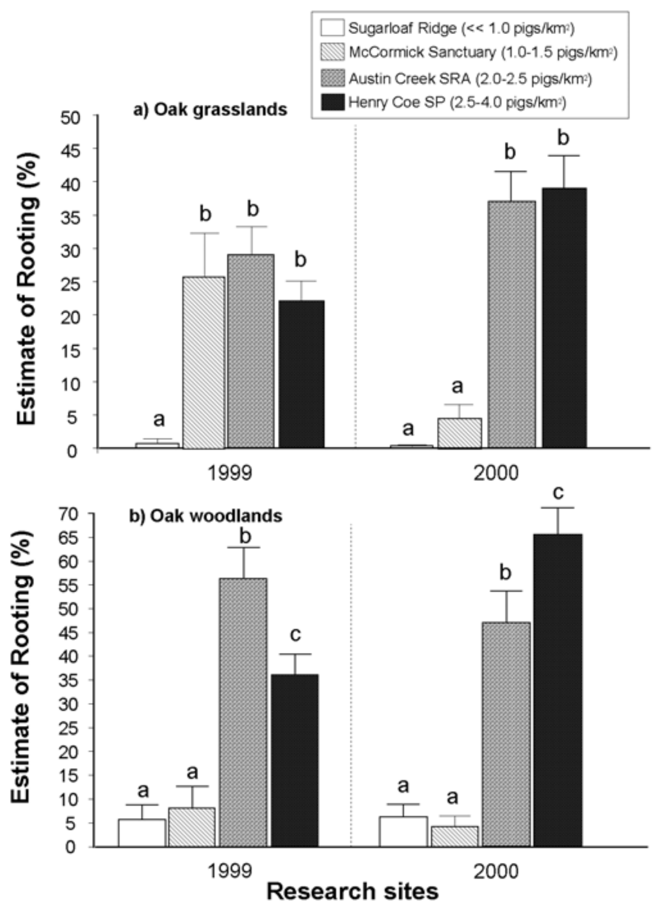

Figure 1—Data on rooting disturbance by wild pigs in (a) oak grassland and (b) oak woodland habitats at the different research sites during the study. Error bars are 1 SE. Different letters between bars indicate significant differences ($\alpha<0.05$).

Data on the effects of rooting on aboveground plant biomass were collected in different ways in 1999 and 2000. For 1999, linear regression analyses of data on natural log transformed dry matter plant biomass by the proportion of a quadrat rooted revealed similar negative relationships between rooting disturbance and aboveground biomass in oak grasslands and oak woodlands *(fig. 2)*. Similarly, linear regression relationships for data from Spring 2000, indicated that as rooting disturbance increased, dry matter plant biomass in rooted biomass plots decreased relative to dry matter plant biomass in unrooted control plots in the same quantitative fashion in grasslands and woodlands *(fig. 2)*.

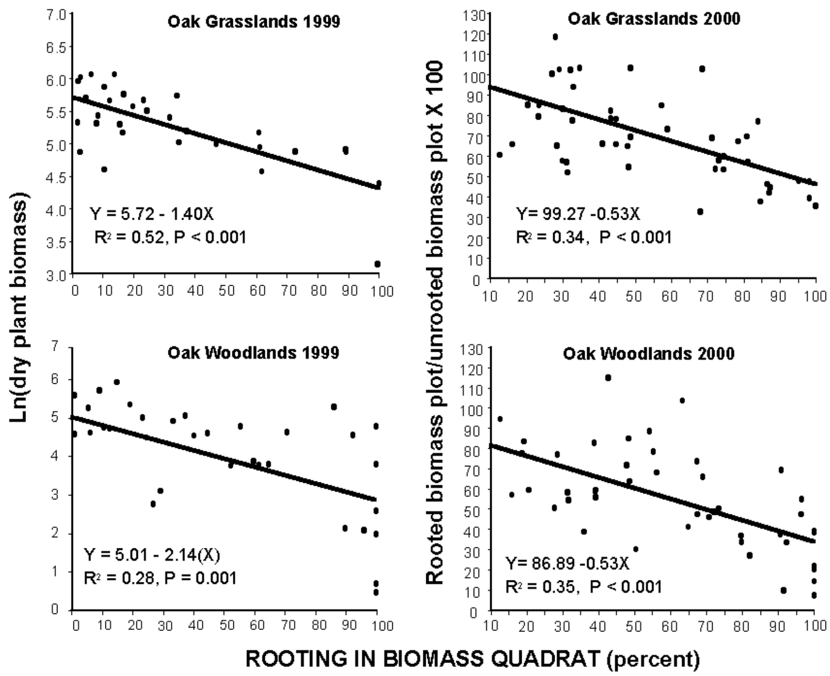

Figure 2—Linear regression relationships between rooting disturbance and aboveground dry plant biomass in oak grassland and oak woodland habitats from 1999 and 2000. Rooting effects on plant biomass were assessed differently in 1999 and 2000.

Tree Regeneration in Oak and Mixed Woodland Habitats

In 1999 and 2000 we measured a combined 15,875 tree seedlings along 80 linear belt transects in oak woodland habitats and 7,385 tree seedlings along 35 linear belt transects in mixed woodland habitats at the four research sites *(table 2)*. Analyses revealed significant variation in mean tree regeneration indices in oak woodland habitats among research sites ($\alpha<0.001$), related to fewer large tree seedlings at sites with higher densities of wild pigs *(fig. 3)*. Pairwise comparisons indicated a higher mean tree regeneration index for Sugarloaf Ridge SP compared to McCormick Sanctuary, Austin Creek SRA and Henry Coe SP (α's<0.028). Tree regeneration indices in oak woodland habitats were similar at the other three research sites. Considering oak tree seedlings only, there also were significant differences in mean tree regeneration indices among research sites ($\alpha=0.001$), related to progressively lower mean oak tree regeneration indices at research sites with increasingly higher wild pig densities *(fig. 3)*. In mixed woodland habitats, however, there was no apparent variation in tree regeneration indices among sites for all tree seedlings (α=0.84, *fig. 3*), or oak tree seedlings only (α=0.10).

Table 2—*Summary of data on tree seedlings enumerated along seedling belt transects in oak woodland and mixed woodlands habitat at each study site during 1999 and 2000.*

	Seedling transects	Total oak seedlings	Large oak seedlings[1]	Total tree seedlings[2]	Large tree seedlings
Oak woodlands 1999					
Sugarloaf Ridge SP	10	569	61	1,266	223
McCormick	10	1,884	83	3,049	244
Austin Creek SRA	10	2,131	28	2,517	58
Henry Coe SP	10	528	19	612	24
Mixed woodlands 1999					
Sugarloaf Ridge SP	5	70	12	1,008	167
McCormick	5	117	26	2,407	457
Austin Creek SRA	5	83	4	423	62
Oak woodlands 2000					
Sugarloaf Ridge SP	10	1,288	129	2,012	415
McCormick	10	2,584	54	3,383	171
Austin Creek SRA	10	1,965	28	2,741	181
Henry Coe SP	10	226	11	295	27
Mixed woodlands 2000					
Sugarloaf Ridge SP	5	150	13	949	234
McCormick	5	231	104	1,435	192
Austin Creek SRA	5	201	6	738	147
Henry Coe SP	5	313	35	435	83

[1] Large tree seedlings were defined as seedlings >200 mm in total size.
[2] All tree seedlings includes oak, conifer, and other hardwood tree seedlings.

Data on tree seedlings along belt transects in habitat exclosure and control plots at Austin Creek SRA and Henry Coe SP were analyzed separately because exclosures were set up one year earlier at Austin Creek SRA. After nearly three years of protection from wild pigs, there were over twice as many tree seedlings along six belt transects in the oak woodland exclosure habitat plot (n=4,869) compared to along six belt transects in the oak woodland control habitat plot (n=2,007) at Austin Creek SRA. Tree seedlings in the oak woodland exclosure habitat plot averaged 96.0 ±0.9 mm compared to 87.0 ±1.7 mm in the oak woodland control habitat plot (α<0.001). In mixed woodland habitat plots at Austin Creek SRA there were nearly twice as many tree seedlings along six belt transects in the exclosure plot (n=1409) compared to along six belt transects in the control plot (n=882). Tree seedlings in the mixed woodland exclosure habitat plot, averaged 98.7 ±2.6 mm compared to 146.5 ±5.9 mm in the mixed woodland control habitat plot (α=0.001). Exclosure habitat plots at Henry Coe SP have been established for two years, but the numbers of seedlings along belt transects in the oak woodland exclosure habitat plots (n=638) were approximately similar to the numbers located along belt transects in oak woodland control habitat plots (n=571). Similarly, the mean sizes of tree seedlings in oak woodland exclosure habitat plots (77.0 ±2.3 mm) were similar to the mean sizes of those in oak woodland control habitat plots (86.9 ±4.7 mm; α=0.10).

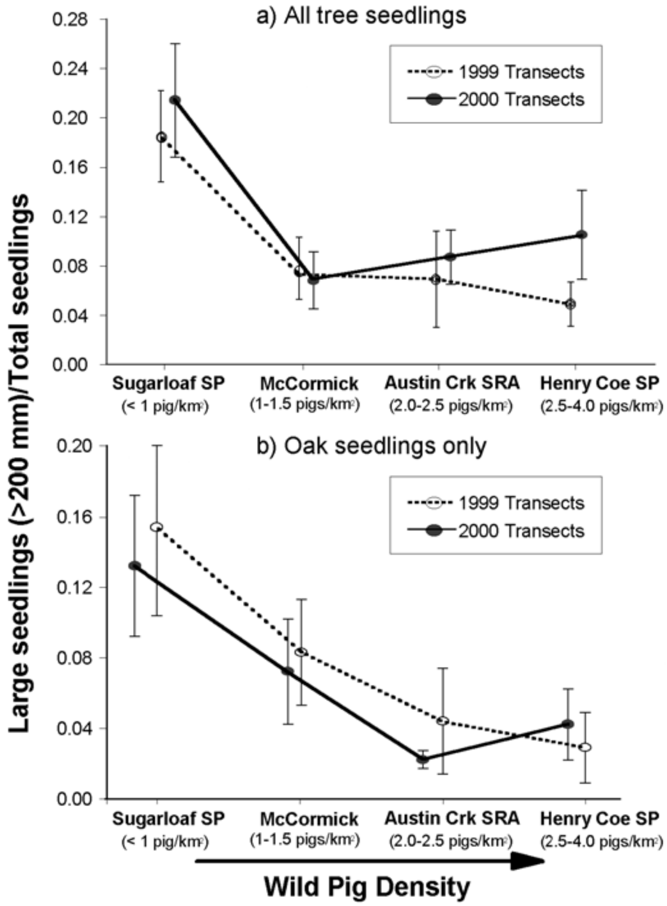

Figure 3—Variation in tree regeneration indices calculated for (a) all tree seedlings, and (b) oak tree seedlings based on data from belt transects at the different research sites.

Data on seedlings in oak canopy exclosure and control plots for experimental oak trees at Austin Creek SRA (*n*=21 trees) and Henry Coe SP (*n*=15 trees) were analyzed separately because some canopy exclosures had been established for one additional year at Austin Creek SRA, and because the species of trees used in canopy experiments were different between the two sites (mostly blue oak at Henry Coe SP, mostly black oak and live oak at Austin Creek SRA). At Austin Creek SRA in spring 2001 there were nearly three times as many seedlings in oak canopy exclosure plots (*n*=620) compared to oak canopy control plots (*n*=223). Average sizes of tree seedlings in the oak canopy exclosures at Austin Creek SRA were larger (81.1 ±1.2 mm) than in oak canopy control plots (74.6 ±2.6 mm; α=0.008). At Henry Coe SP we counted approximately similar numbers of tree seedlings in oak canopy exclosure plots (*n*=20) as in oak canopy control plots (*n*=32). Nevertheless, sizes of tree seedlings in the canopy exclosure plots (76.8 ±6.4) were larger than in the canopy control plots (60.8 ±4.2 mm; α=0.034).

Oak Acorn Survival and Oak Canopy Exclosures

Results from acorn survival monitoring during fall 1998 indicated that most acorn drop on the plots occurred from late September to mid-October. We detected fewer acorns on the control plots compared to the experimental plots on each of the four analysis dates (Paired t-test α's<0.001 for each of four comparisons). However, over 99 percent of the approximately 23,000 acorns observed on the plots in fall 1998 were either aborted or rotten. Data on acorn survival from fall 1998 are therefore of limited interest relative to potential wild pig foraging effects.

Acorn numbers were monitored in control and experimental plots beneath 15 oak trees at Henry Coe SP and 15 oak trees at Austin Creek SRA in fall 1999. Most of the acorn drop in 1999 occurred during late October and November when proportionally more of the acorns noted on the survival plots in 1999 were mature compared to 1998. At Austin Creek SRA, the total numbers of mature acorns in plots under the 15 trees ranged from 544 in September to 2,408 in mid December *(fig. 4)*. At Henry Coe SP, the total numbers of acorns in plots under the 15 trees ranged from 1892 in September to 4,960 in November *(fig. 4)*. At both Austin Creek SRA and Henry Coe SP numbers of acorns were initially higher in control plots than in experimental plots, but were less numerous in experimental plots than in control plots by midway through the monitoring period *(fig. 4)*. Analysis of data on acorn numbers beneath oak trees by repeated measures ANOVA indicated that fewer acorns survived on control plots than on experimental plots by the end of the monitoring period in mid December (α=0.001).

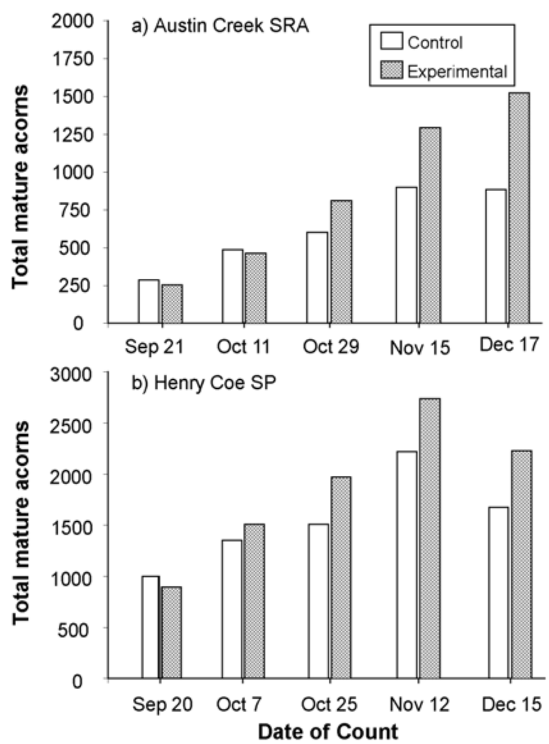

Figure 4—Results from oak canopy experiments on acorns observed on different types of monitoring plots at (a) Austin Creek SRA, and (b) Henry Coe SP during fall 1999. Data are from 16 and 15 experimental trees at Austin Creek SRA and Henry Coe SP, respectively.

Discussion

In this study we are using a combination of experimental and descriptive methods to assess multiple hypotheses related to the potential ecological effects of wild pigs on native ecosystems. After two years of research, our results indicate that rooting disturbance by wild pigs may exceed 35-65 percent annually in areas with high-density pig populations. Rooting disturbance by wild pigs contributed to significant declines in aboveground biomass productivity *(fig. 2)*, which may reduce resource availability for a wide variety of terrestrial vertebrates and invertebrates. Rooting by wild pigs was much more widespread at research sites with relatively high pig density compared to sites with relatively low pig density *(fig. 1)*. This is important because rooting disturbance may potentially alter competitive relations among plants to a greater degree in areas where pig densities are relatively high. For example, the intermediate disturbance hypothesis predicts that species diversity/community heterogeneity should be highest in areas with intermediate levels of disturbance compared to areas with very low or very high disturbance. This may be important from a historical perspective because there was another large omnivore, the grizzly bear (*Ursus arctos*), present in California until the 1920s. Historical accounts indicate that grizzly bears once consumed considerable acorn mast and "grubbed" extensively for forage in and around California's oak woodland ecosystems (Pavlik and others 1992). The last free ranging grizzly bear in California was killed in 1922. Related to the grizzly bear's taste for acorns and grubbing behavior that may have been very similar to rooting by wild pigs (Tardiff and Stanford 1998), it has been suggested that wild pigs are the ecological equivalent of the now extinct grizzly bear in California (Work 1993). According to this hypothesis, some intermediate level of acorn foraging and rooting disturbance by wild pigs may replace the activities of grizzly bears as an important source of natural disturbance in oak woodland ecosystems. This idea remains to be quantitatively assessed.

Our data suggest that high levels of rooting by wild pigs in areas where densities exceed 2.0 pigs/km^2 is contributing significantly to reduced tree seedling regeneration in oak woodland ecosystems in California *(fig. 4)*. It was notable that most of the large seedlings encountered in oak woodlands at both Austin Creek SRA and Henry Coe SP were actually stump sprouts and not seedlings that survived from germinated acorns. Also, experimental data from both habitat plot and oak canopy exclosures at Austin Creek SRA suggest that the rooting activities of wild pigs significantly reduce tree seedling survival; the lack of differences in absolute numbers of tree seedlings in exclosure compared to control plots in habitat and oak canopy experiments at Henry Coe SP may have been due to the relatively short duration the exclosures have been present at this site. Mule deer (*Odocoileus hemionus*) also consume young oak seedlings, however, and it is possible that reduced foraging by deer in exclosure compared to control habitat plots contributed to higher seedling numbers in the exclosure woodland habitat plot at Austin Creek SRA. However, we commonly observed deer or their sign in exclosure and control habitat plots at both Austin Creek SRA and Henry Coe SP, suggesting that deer had ready access to both areas. Deer may not have had full access to all oak canopy exclosure plots, however, because these exclosures were relatively small (3x3 m) and some were situated directly beneath the canopies of oak trees.

Data on numbers of acorns associated with oak canopy experiments indicate that acorn consumption by wild pigs contributes to both reduced acorn survival to potential germination and reduced forage availability for wildlife *(fig. 4)*. Data on mature acorns from our 1999 oak canopy experiments indicated that control monitoring plots initially had higher numbers of acorns than exclosure plots in September, but that pattern was reversed by October, and progressively fewer mature acorns were located on control compared to exclosure monitoring plots from October through mid December. Rooting by wild pigs was observed within control plots on multiple occasions, suggesting that differences in acorn survival may have been due to foraging by wild pigs. As previously noted, however, it is uncertain whether deer foraged inside of all oak canopy exclosures.

Management Implications

After two years of comparative and experimental research we have been able to quantitatively assess several aspects of the rooting and foraging activities of wild pigs. Data indicate that this introduced species may be reducing tree regeneration potential and forage availability for native wildlife in California's oak woodland ecosystems. Additional longer term monitoring is underway for assessing the effects of wild pigs on plant and terrestrial vertebrate communities. The most important finding from the study to date is that wild pig rooting and foraging is significantly reducing already low levels of oak regeneration in California (McCreary 1990). Wild pigs are only one potential agent of change or disturbance impinging on oak woodlands in California, however, which continue to experience degradation by agricultural development, livestock grazing, and disease. Because it will be difficult to significantly reduce pig numbers in natural areas where hunting is prohibited, the activities of expanding wild pigs will continue to exacerbate already difficult management and conservation problems associated with California's unique oak woodland ecosystems.

Acknowledgments

Renee Pasquinelli, Marla Hastings, Kay Robinson, Tracey Becker, Chaz Pothast, Joanne Karlton, and Barry Breckling of California Department of Parks and Recreation provided research access and logistical support at state park research sites. Craig Anderson facilitated research at McCormick Sanctuary. Many technicians assisted with field research, but Juanita Constible and Neil Kadrmas provided invaluable multiple-year assistance. Project funding from May 1998 to June 2000 was provided by the California Department of Fish and Game (FG-7113-WM). Funding from fall 2000 to fall 2005 is being provided by the Integrated Hardwood Range Management Program.

References

Barrett, Reginald H. 1978. **The feral hog on the Dye Creek Ranch, California.** Hilgardia 46: 281-355.

Giusti, Gregory A. 1993. **Wild pig expansion and economic impacts in Mendocino County, California.** In: Conference summaries of the wild pig in California oak woodland: ecology and economics; 1993 May 25-26; San Luis Obispo, California. Berkeley, CA: Integrated Hardwood Range Management Program; 23-25.

Graves, W. C. 1980. **Annual oak mast yields from visual estimates.** In: Plumb, Timothy R., technical coordinator. Proceedings of the symposium on the ecology, management and utilization of California oaks; 1979 June 26-28; Claremont, CA. Gen. Tech. Rep. PSW-RP-44. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 270-274.

Kotanen, Peter M. 1995. **Responses of vegetation to a changing regime of disturbance: effects of feral pigs in a California coastal prairie.** Ecography 18: 190-199.

Mayer, John M.; Brisbin, I. Lehr. 1991. **Wild pigs in the United States: their history, comparative morphology, and current status.** Georgia: University of Georgia; 313 p.

McCreary, Douglas D. 1990. **Native oaks: the next generation.** Fremontia 19: 44-47.

Oliver, W. L. R.; Brisbin, I. Lehr. 1993. **Introduced and feral pigs: problems, policy, and priorities.** In: Oliver, W.L.R., ed. Pigs, peccaries and hippos. International Union Conservation of Nature and Natural Resources, Gland, Switzerland.

Pavlik, Bruce M.; Muick, Pamela C.; Johnson Sharon G.; Popper, Marjorie. 1992. **Oaks in California.** California: Cachuman Press; 184 p.

Schauss, Martha E.; Coletto, Henry J.; Kutilek, M.J. 1990. **Population characteristics of wild pigs, *Sus scrofa* in eastern Santa Clara County, California.** California Fish and Game Quarterly 48: 68-77.

Sweitzer, Richard A. 1998. **Conservation implications of feral pigs in island and mainland ecosystems and a case study of feral pig expansion in California.** In: Baker, Rex, O.; Crabb, Charles, A., technical coordinators. Proceedings of the 18th vertebrate pest conference, Vertebrate Pest Council; 1998 March 2-5; Costa Mesa, California. University of California, Davis, CA; 26-34.

Tardiff, S.E.; Stanford J.A. 1998. **Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability.** Ecology 7: 2219-2228.

Waithman, John. D.; Sweitzer, Richard A.; Brinkhaus, Amy J.; Gardner, Ian A.; Drew, John D.; Van Vuren, Dirk H.; Boyce, Walter M. 1998. **Range expansion, population sizes, and conservation implications of introduced wild pigs (*Sus scrofa*) in California.** The Journal of Wildlife Management 63: 298-308.

Work, George. 1993. **A rancher's view of the wild pig as an economic and ecological asset to the ranching enterprise.** In: Conference summaries of the wild pig in California oak woodland: ecology and economics; 1993 May 25-26; San Luis Obispo, California. Berkeley, CA: Integrated Hardwood Range Management Program; 5.