

Ecosystem change along a woody invasion chronosequence in a California grassland

E.S. Zavaleta^{a,b,*}, L.S. Kettley^a

^a*Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA*

^b*Carnegie Institution of Washington, 260 Panama St, Stanford, CA 94305-5020, USA*

Received 17 December 2003; received in revised form 6 July 2005; accepted 22 November 2005
Available online 18 January 2006

Abstract

Woody species have increased in abundance in many grassland ecosystems during the last century. To investigate the consequences of *Baccharis pilularis* encroachment into coastal California grasslands, we established a chronosequence of sites naturally invaded by *Baccharis* zero to 25 years ago. Increasing above- and below-ground biomass increase along the chronosequence drove increases in ecosystem N sequestration of ~700% and in C storage of over 125%. Colonization by oaks (*Quercus agrifolia*) and other woody species at sites colonized by *Baccharis* >15 years ago indicate that the progressive ecosystem changes observed in chronosequence reinforce woody dominance and associated changes at shrub-invaded sites.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Woody invasion; California grassland; Carbon storage; Nitrogen; *Baccharis pilularis*; *Quercus agrifolia*; Climate change; Ecosystem engineer

1. Introduction

A number of studies have linked the presence and abundance of novel, keystone, and engineer species to rates and magnitudes of ecosystem processes (Jones et al., 1997; Chapin et al., 2000; Diaz and Cabido, 2001). However, there have been few, long-term investigations of the time course of ecosystem change following new colonizations and expansions of such species. Studies of chronosequences, series of sites that differ from one

*Corresponding author. Current address: Environmental Studies Department, University of California, Santa Cruz, USA Tel.: +1 831 459 5011; fax: +1 831 459 4015.

E-mail address: zavaleta@ucsc.edu (E.S. Zavaleta).

another primarily as a result of time elapsed since focal events, have been used to assess rates of ecosystem development (Vitousek and Farrington, 1997), primary succession (Fastie, 1995; Zarin and Johnson, 1995; Lichter, 1998), secondary succession (Ranger et al., 1995; Norland and Hix, 1996; Uriarte, 2000) and ecosystem recovery following disturbance (Carreira et al., 1994; Bormann et al., 1995; Pardo et al., 1995). Temporally explicit studies of species additions to ecosystems could answer questions such as: How does ecosystem response evolve as invading organisms mature? Are ecosystem changes progressive, or do they entail step changes at particular phases? How are successive ecosystem responses to a species addition linked to one another? Chronosequence studies can also provide insight into the long-term and landscape-scale implications of community shifts detected in short-term, plot-scale experiments.

Woody invasions of herb-dominated ecosystems are excellent model systems for study of the links between vegetation shifts and long-term ecosystem change for several reasons. Woody invaders and herbaceous dominants differ greatly in a range of traits important to ecosystem function, including rooting depth and distribution, phenology, life history, and structure (Diaz and Cabido, 1997). Woody invasions therefore can strongly influence ecosystem biogeochemistry, composition, and physical environments (Belsky et al., 1989; Wilson and Agnew, 1992; Jones et al., 1997; Schlesinger and Pilmanis, 1998), potentially producing feedbacks to regional biological processes and climate (Schlesinger et al., 1990). Because woody species are typically long-lived, they have the potential to drive progressive changes in ecosystem function for decades as they mature and senesce. Moreover, woody encroachment of grasslands has accelerated during the 20th century in several parts of the world (Polley et al., 1996). Some of these invasions appear to have been driven by anthropogenic climate and atmospheric changes (Nielson, 1986; Williams et al., 1987; Polley et al., 1996; Brown et al., 1997), while others reflect the impacts of livestock grazing (Archer et al., 1988; Brown and Archer, 1989; Reid and Ellis, 1995), altered disturbance regimes (Calder et al., 1992), and exotic species introductions (Brown and Carter, 1998). Increasing woody plant abundance could represent an important portion of the global carbon budget (Houghton et al., 1996), (Schimel et al., 2000; Pacala et al., 2001), but relatively little is known about the rates and magnitudes of biogeochemical changes in ecosystems undergoing transition from grassland to woody dominance. Improving understanding of how woody encroachment alters the course of ecosystem structure and function is therefore of current conservation and policy interest.

To provide insight into the potential long-term consequences of *Baccharis* encroachment, we examined patterns of production, standing biomass, carbon and nitrogen storage, community composition, and soil moisture along a 25-year chronosequence of *Baccharis*-invaded sites. We expected root production, exudation, and turnover in shrubs together with low decomposition rates in deep soils to lead to progressive accumulation of deep soil carbon. We also expected progressive increases in above-ground carbon pools to accompany the development of shrub stands. We expected nitrogen (N) to become increasingly sequestered in woody tissue, evergreen leaves, roots, and litter, leading to declines in litter quality that might in turn reduce decomposition rate and increase carbon immobilization in recalcitrant litter and soil organic matter. Finally, we expected additional, progressive changes in the availability of resources such as light and moisture (Hobbs and Mooney, 1986) to impact the understory plant community, including the establishment of new woody plants such as *Baccharis* and successional oaks (*Quercus* sp.) (McBride, 1974).

2. Methods

2.1. Study site

This study was conducted in an annual, exotic-dominated grassland at Stanford University's Jasper Ridge Biological Preserve in the interior foothills of the central coast range south of San Francisco, California, USA. The site has a Mediterranean-type climate with summer droughts typically extending from April to October and winter rains extending from November to March. Mean annual precipitation at the site is 605 mm; in a typical year, daily average temperatures range from a minimum of 2–4 °C in winter to a maximum of 25–27 °C in midsummer (unpublished, Jasper Ridge Biological Preserve data records).

2.2. Shrub invasion chronosequence

Previous work indicates that *Baccharis* shrubs >10-years old cannot be reliably aged by direct methods (Hobbs and Mooney, 1986). A series of high-resolution historical aerial photographs taken of the Jasper Ridge Biological Preserve was used to identify (1) fifteen *Baccharis pilularis* individuals or stands that ranged in approximate age from 5 to 25 years and (2) 15 uninvaded grassland stands. All stands were within a 0.25 km² area. To minimize differences in resource availability and environmental conditions, all stands were located on flat or nearly flat areas away from abrupt topographic features, on sandstone soils > 50 cm depth. The site has been protected since 1960 as an academic preserve; before that, portions of it experienced surface disturbances such as livestock grazing, mowing, and vehicle compaction (personal communication, Nona Chiariello, Jasper Ridge Biological Preserve). All stands selected have vegetation limited to annual-dominated grassland and *Baccharis* shrubs.

Ground-truthing indicated that shrubs reach approximately 3–5 years of age (>0.5 m diameter) before becoming reliably visible in the aerial photographs. Colonization dates were estimated as the first date that an individual appears in an aerial photograph +4 years. Because of several 1–4 year gaps in the historical photo record, shrub ages may be underestimated by as much as 4 years. The 15 shrub-invaded stands were grouped into age-classes with medians at 5-year intervals from 5 to 25 years. Two sites were invaded ~5 years ago, three sites each were invaded ~10, 15, or 20 years ago, and four sites were invaded ~25 years ago. A single, focal shrub was selected in each *Baccharis* stand. In some instances, the focal shrub was the only shrub present; in other instances the focal shrub was a randomly selected individual at the edge of a small cluster. The 15 grassland sites were each located 4 m away from the perimeter of one of the focal shrubs in a direction chosen to minimize differences in topography, aspect, elevation, soil type, and disturbance history and to maintain distance from roads, paths, and other woody vegetation.

2.3. Litter and biomass samples

All litter and above-ground herbaceous biomass was collected from two circular subplots totaling 37 cm² at each of the 30 stands. In grassland stands, the subplots were located 0.5 m to either side of the stand center, on a line tangent to the perimeter of the closest shrub. In shrub stands, the two subplots were located 0.5 m to either side of a point

chosen in a random direction from the shrub's central stem, at a point halfway between the central stem and the canopy edge. Harvest dates were staggered between grassland and shrub stands to capture peak herbaceous biomass (Shaw et al., 2002) at the two types of sites, with grassland sites sampled on 24 April 2000 and shrub sites sampled 2 weeks later. Samples were sorted to species, oven-dried at 65 °C for 72 h, and weighed. Litter was divided into <0.5, 0.5–1.0, and 1.0–2.0 cm diameter size classes, with all herbaceous litter in the smallest size class, before drying. Because the herbaceous vegetation was dominated by annual species, current-year herbaceous biomass was used as an estimate of understory above-ground net primary productivity (ANPP).

Woody ANPP and biomass were sampled for one randomly selected shrub in each age class. On 30 April 2000, all new leaves and shoots were harvested from within a 12.5° wedge-shaped slice of an imaginary vertical cylinder centered at the central stem of the study shrub and extending out to the canopy edge in a randomly chosen direction. Samples were oven-dried for 72 h at 70 °C and weighed. This index of AA underestimates actual ANPP by excluding diameter increments to stems and is therefore used only as a relative measure. In December 2000, an additional wedge from each shrub was harvested completely. Samples were sorted to green material, live wood, and dead wood to obtain estimates of total woody biomass. Samples were oven-dried at 65 °C for 1 week and weighed. Subsamples of green, live, and dead wood from the youngest (age 5) and oldest (age 25) age classes were ground to pass through a 40-mesh screen (Wiley mill) and analysed for C and N content (Carlo-Erba 1108 elemental analyser). ANPP was crudely estimated by computing the mean annual increment in standing biomass between age classes. This estimated woody ANPP was combined with measured herbaceous ANPP to calculate total ANPP. Woody and total ANPP are underestimated by this method because it does not account for turnover of above-ground tissue.

2.4. Soil and root cores

A single soil core was collected from each of the 30 stands on 3 April 2000 to measure gravimetric soil moisture, carbon and nitrogen content, and root biomass and chemistry. Cores (2.5 cm diameter) were collected from the center of grassland stands and mid-way between stems of targeted shrubs and their canopy edges and partitioned into 0–15, 15–30, and 30–47 cm depth segments. Soils were homogenized and gravimetric moisture content of subsamples was determined. Other subsamples were dry-sieved through 2, 1, and 0.5 mm-mesh sieves then hand-picked with tweezers to remove roots, litter, and rocks. The resulting samples were ground for 24 h on a roller-bar grinder and subsampled for elemental analysis.

The remaining soil in each bulk sample was weighed, decanted to remove rocks, and wet-sieved to retrieve plant matter. The plant matter was then suspended in water and hand-picked with tweezers to remove litter and debris and to isolate roots. Root samples were oven-dried for 72 h at 70 °C, weighed, finely snipped with scissors, and subsampled for elemental analysis. All elemental chemistry analyses were done on a Carlo-Erba Model 1108 elemental analyser coupled to a continuous flow mass spectrometer.

Bulk density was measured in January 2001 in one plot from each of the six age groups (0–25). Pits were dug and horizontal cores taken from the midpoint of each of the three sampled depth ranges. Bulk density measures were used to estimate soil C and N content on a mass basis. All 30 stands were cored a second time in January 2001 with a 2.2 cm corer to obtain soil samples for measuring soil pH.

2.5. Statistical analysis

Variables were log transformed using $X' = \log_{10}(X + 1)$ when necessary to meet model assumptions. Herbaceous biomass was square-root transformed using $X' = (X + 1)^{0.5}$ because log transformation did not yield normally distributed data.

To analyse the effects of time since shrub establishment, data were analysed using stepwise regression (Zar, 1996). Stepwise regression and comparison of R^2 values across models indicated whether a linear, second-power, or asymptotic ($y = a + b/x$) curve provided the best fit to the data. An F statistic is reported to indicate cases where a nonlinear curve provided a significantly better fit than a line. The stepwise procedure allowed discrimination between variables that continued to change with time since woody establishment and variables that reached new equilibria <25 years after shrub establishment or otherwise responded nonlinearly to time since shrub establishment. All reported R^2 values are corrected (adjusted) (Zar, 1996). Outliers were treated by comparing (1) results with the outlier data including (2) results with the outlier value recoded to fall 10% beyond the next most extreme value in that age class (Tabachnick and Fidell, 1996). Where the shape of the relationship was not affected by recoding the outlier, only the result with the original outlier value is reported.

3. Results

3.1. Above-ground productivity and species composition

Contributions to woody ANPP came primarily from *B. pilularis* and secondarily from poison oak (*Toxicodendron diversilobum*) and live oak (*Quercus agrifolia*), both of which contributed biomass only in the oldest age class. Total woody ANPP showed no clear pattern of response, but *Baccharis* ANPP dropped off sharply in year 25 and was largely replaced by *Q. agrifolia* and *T. diversilobum* (Fig. 1). Three of the four 25-year shrub sites in this study contained seedlings or saplings of *Q. agrifolia*, a native oak, while two of the 15-year sites and one of the 20-year sites contained small *Q. agrifolia* seedlings.

Declines in total ANPP that occurred with *Baccharis* age ($p = 0.025$, $R_{\text{adj}}^2 = 0.49$) were driven by declines in herbaceous ANPP ($p < 0.001$, $R_{\text{adj}}^2 = 0.37$) (Fig. 2). Biomass of native herbaceous species remained constant across the chronosequence, whereas that of exotic species declined with shrub age. As a result, the native fraction of herbaceous biomass tended to increase linearly with time since invasion ($p = 0.055$, $R_{\text{adj}}^2 = 0.09$). However, individual sites in every age class varied strongly in native fraction of understory biomass, illustrating that factors other than shrub age exert strong influence on native species performance in the understory.

3.2. Woody biomass and C storage

Standing above-ground woody biomass increased rapidly and linearly with time since shrub establishment (Fig. 3a) ($p = 0.007$, $R_{\text{adj}}^2 = 0.92$). This increase was driven by rapid accumulation of dead wood in the canopy, while live woody biomass peaked at year 15 then declined (Fig. 3b). As a result of these rapid biomass increases (above-ground C concentrations did not vary with shrub age), estimated total C stored in standing above-ground woody

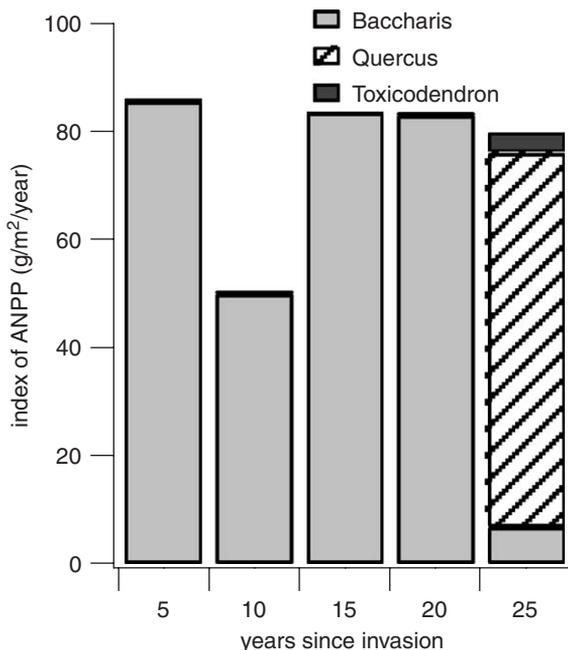


Fig. 1. The influence of time since shrub establishment on index of total woody above-ground NPP (ANPP) and species composition of woody ANPP.

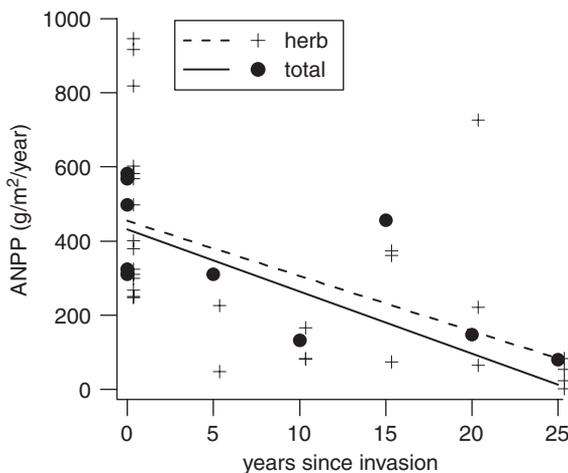


Fig. 2. The influence of time since shrub establishment on herbaceous ($n = 30$) and total (herbaceous + woody, $n = 10$) above-ground net primary productivity (ANPP). Herbaceous ANPP: $y^{0.5} = 20.7 - 0.51x$; total ANPP: $y = 431 - 16.8x$.

biomass increased strongly with time since invasion (Table 1). The ratio of green (leaves and green stems) to woody tissues in shrubs responded asymptotically, declining rapidly through year 10 and slowly thereafter ($p < 0.01$, $R_{adj}^2 = 0.96$).

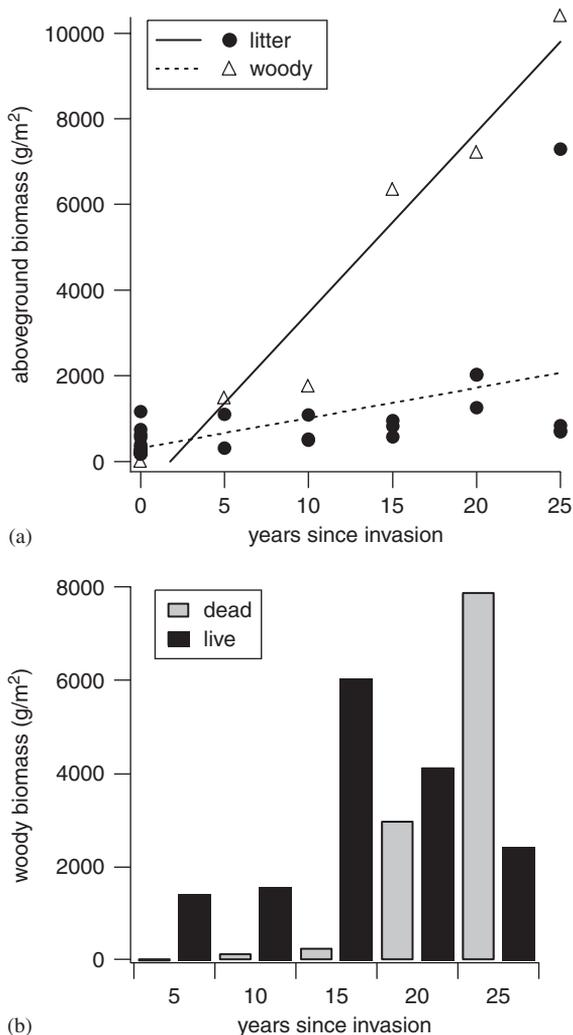


Fig. 3. The influence of time since shrub establishment on (a) total above-ground standing biomass of all woody species ($y = -1555 + 466x$) and surface litter biomass ($y = 304.6 + 70.44x$), and (b) contributions of live and dead wood to above-ground standing biomass of woody species.

3.3. Litter biomass and carbon storage

Total surface litter biomass increased linearly with time since invasion (Fig. 3a) ($p = 0.003$, $R_{\text{adj}}^2 = 0.25$). An outlier data point at 25 years has high leverage but does not affect the finding that the relationship is linear. This response was driven by progressive increases in coarse litter biomass, while litter biomass in the smallest size class (<0.5 cm) increased for 15 years then declined to pre-invasion levels by year 25 ($p \ll 0.001$, $R_{\text{adj}}^2 = 0.32$). Increases in total litter biomass drove linear increases in total C stored in litter (Table 1) ($p = 0.005$, $R_{\text{adj}}^2 = 0.22$). Litter C concentrations did not vary significantly with shrub age.

Table 1

The influence of time since *Baccharis* establishment on mean carbon sequestration in biomass, litter, and soil

	Years since establishment					
	0	5	10	15	20	25
<i>Aboveground biomass</i>						
Dead wood ^a	0	14.7	84.1	145.7	1575	4148
Live wood	0	549.5	752.8	2970	2026	1215
Green woody	0	191.9	61.6	148.1	118.1	41.3
Other woody	0	13.8	7.33	21.3	37.3	42.4
Herbaceous ^b	176.2	48.5	39.2	95.8	120.4	14.3
Subtotal	176.2	818.4	945.03	3380.9	3876.8	5461
<i>Roots</i>						
0–15 cm	71.7	65.8	144.3	112.6	115.5	96.4
15–30 cm	19.5	32.8	51.8	911.8	302.7	61
30–47 cm	8	13.2	72.3	49.8	32.5	896.4
Subtotal	99.2	111.8	268.4	1074	450.7	1054
<i>Litter</i>						
<0.5 cm	138.3	183.7	250.1	301.7	453.5	200.7
0.5–1.0 cm	5.9	80.3	0	4.1	30.2	456.9
1.0–2.0 cm	0	0	0	0	210.7	397.2
Subtotal	144.2	264	250.1	305.8	694.4	1055
<i>Soil</i>						
0–15 cm	2635	2765	3422	3661	3414	3541
15–30 cm	1696	2060	2133	2105	2258	2235
30–47 cm	1603	1678	1528	1703	2010	2050
Subtotal	5934	6504	7083	7469	7682	7826
Total	6353	7698	8546	12230	12700	15400

All values are in gC/m².

^a“Dead wood” refers to standing litter >2.0 cm in diameter. “Green woody” refers to new, unligified shrub growth, while “live wood” refers to living, lignified tissue. “Other woody” includes material that could not be conclusively placed in one of the other three categories.

^bA mean %C value of 42.7, calculated from 8 samples of each of the three dominant species in nearby grassland, is used and provides a rough estimate of total herbaceous biomass values (Zavaleta, unpubl. data).

Total litter C:N declined with time since invasion ($p = 0.016$, $R_{adj}^2 = 0.16$). This increase in overall litter quality was driven by quality increases in the smallest litter size class, which had its highest C:N values at shrub-free sites and lower values under shrubs. Over time, surface litter dynamics were therefore characterized by both large accumulations of coarse litter with high C:N and smaller eventual declines in fine litter biomass as it increased in quality.

3.4. Below-ground biomass and carbon storage

While soil pH increased linearly with shrub age ($p = 0.005$, $R_{adj}^2 = 0.22$), mean pH changed by <0.2, from 6.03 to 6.17. Total carbon (gC/m²) in the top 47 cm of soil

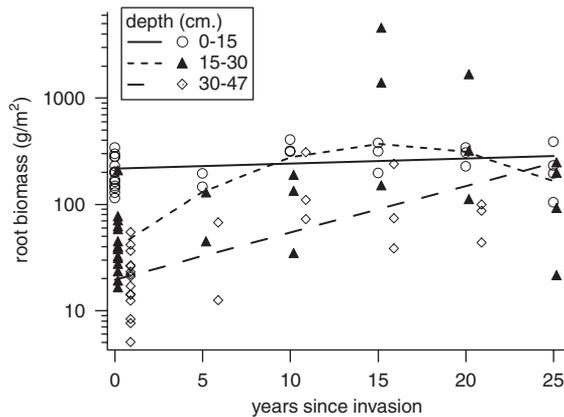


Fig. 4. The influence of time since shrub establishment on root biomass at three depth intervals. 0–15 cm: $\log(y+1) = 2.314 + 0.005x$; 15–30 cm: $\log(y+1) = 1.595 + 0.125x - 0.004x^2$; 30–47 cm: $\log(y+1) = 1.313 + 0.43x$.

increased linearly with time since woody establishment ($p = 0.013$, $R_{\text{adj}}^2 = 0.17$). With a single outlier recoded, the relationship is stronger ($p < 0.001$, $R_{\text{adj}}^2 = 0.38$). Within individual depth intervals, soil C increases were linear but were stronger in surface than in subsurface soils (Table 1). Based on our limited sampling, bulk density did not change with shrub age at any depth sampled ($p > 0.5$). Changes in total soil carbon thus appear entirely due to increases in soil %C. The mean increase in total soil carbon at 25 years of 1892 g/m^2 represents a 32% increase over pre-invasion levels.

Total root biomass increased asymptotically with time since woody establishment. While there was not a significant F associated with the addition of a quadratic term, a second-order model provided a more satisfactory fit to the asymptotic trend in the means based on visual inspection ($p < 0.001$, $R_{\text{adj}}^2 = 0.41$). Responses of root biomass were distinct at each depth interval (Fig. 4). From 0 to 15 cm soil depth, root biomass did not increase significantly with shrub age. However, recoding of a single outlier yielded a stronger relationship ($p = 0.009$, $R_{\text{adj}}^2 = 0.20$). From 15 to 30 cm soil depth, root biomass peaked at 15 years then declined ($p < 0.001$, $R_{\text{adj}}^2 = 0.458$). From 30 to 47 cm soil depth, root biomass increased linearly, with a large increase in year 25 ($p < 0.001$, $R_{\text{adj}}^2 = 0.42$).

The size of the root carbon pool increased because of both increasing root biomass and increasing %C in root tissue. Across depths, 18% of the root C increase was due to higher root %C. Root tissue %C increased strongly with time since woody establishment at all depths, most likely due to increasing proportions of woody roots ($p \ll 0.001$, $R_{\text{adj}}^2 = 0.62$). Total root carbon pool size increased linearly with time since woody establishment ($p < 0.001$, $R_{\text{adj}}^2 = 0.36$), mainly due to total root C increases between 15 and 47 cm soil depths (Table 1).

3.5. Nitrogen pools and soil moisture

Nitrogen immobilization in live and dead biomass increased progressively with time since woody establishment (Table 2). Total nitrogen in litter increased linearly over time ($p \ll 0.001$, $R^2 = 0.59$) due to increases across all three litter size classes. Total nitrogen in roots also increased over time, though a maximum value was reached at year 15.

Table 2

The influence of time since *Baccharis* establishment on nitrogen pools in biomass and litter and on total soil nitrogen

	Years since establishment					
	0	5	10	15	20	25
<i>Aboveground biomass</i>						
Live wood	0	3.51	4.82	19	13	7.78
Dead wood	0	0.157	0.897	1.55	16.8	44.2
Green woody	0	4.26	1.46	3.4	2.9	1.07
Other woody	0	0.19	0.101	0.294	0.515	0.586
Herbaceous ^a	6.08	1.67	1.35	3.31	4.15	0.492
Subtotal	6.08	9.79	8.63	27.6	37.4	54.1
<i>Roots</i>						
0–15 cm	2.5	2.1	4	4.2	3.5	3.3
15–30 cm	0.6	1.9	1.3	7.1	3.3	1.9
30–47 cm	0.3	0.4	1.3	0.9	0.6	6.3
Subtotal	3.4	4.4	6.6	12.2	7.4	11.5
<i>Litter</i>						
<0.5 cm	2.7	5.1	7.1	9	12.2	6.3
0.5–1.0 cm	0	2.1	0	0.1	0.4	7.1
1.0–2.0 cm	0	0	0	0	5.1	5
Subtotal	2.7	7.2	7.1	9.1	17.7	18.3
Total in biomass	12.2	21.4	22.3	48.9	62.5	83.9
<i>Soil</i>						
0–15 cm	255	256	296	316	297	304
15–30 cm	183	217	224	216	233	221
30–47 cm	177	181	176	193	212	204
Total in soil	603	657	696	726	743	729

All values are in gN/m².

^aA mean %N value of 1.225, calculated from 8 samples of each of the three dominant species in nearby grassland, is used and provides a rough estimate of total herbaceous biomass values (Zavaleta, unpubl. data).

A quadratic function did not provide a significantly better fit than a linear model but did improve R^2 and concurred with the asymptotic trend in mean values ($R_{\text{adj}}^2 = 0.45$ vs. 0.36) ($p < 0.001$, $R_{\text{adj}}^2 = 0.45$). Total N in biomass increased nearly seven-fold from shrub-free grassland to 25-year *Baccharis* sites (Table 2).

Total soil nitrogen also increased over time, though mean soil nitrogen ceased to increase after 15 years ($p = 0.002$, $R_{\text{adj}}^2 = 0.26$) (Table 2). Rates of soil N accumulation were higher in the top 30 cm of soil than between 30 and 47 cm. Soil moisture across the depths sampled increased with time since shrub establishment ($p < 0.01$, $R_{\text{adj}}^2 = 0.27$).

4. Discussion

Significant and consistent changes occurred across the 25-year woody encroachment chronosequence in ecosystem C storage, biomass and litter N pools, productivity, and soil

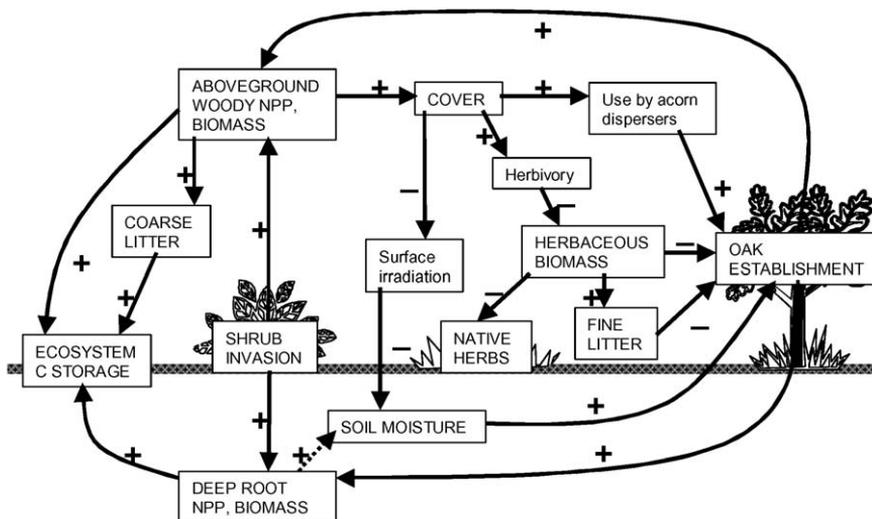


Fig. 5. Hypothesized relationships among *Baccharis* establishment, ecosystem productivity and biomass, woody succession, and C storage. Components in uppercase letters were measured in this study. Components in lowercase letters were not measured in this study but have been addressed by previous research. + and – symbols signify positive and negative relationships, respectively, between components. Arrows indicate the hypothesized direction of influence.

moisture. Some of these changes, though based on relatively limited sampling, may explain shifts in the understory community that include increases in the relative abundance of native herbs and the establishment of native oaks. The latter result suggests that the effects of *Baccharis* establishment on ecosystem properties may include facilitated succession to oaks with life-spans of centuries and the potential to drive larger ecosystem changes. A conceptual model illustrates positive feedbacks among shrub encroachment, ecosystem productivity and biomass, woody succession, and C storage (Fig. 5). In this model, both direct effects of *Baccharis* production and longer-term increases in oak establishment contribute to progressive gains in ecosystem C.

Woody and herbaceous dominance in grassland–woodland systems have been described as alternative stable ecosystem states, each of which is maintained by self-reinforcing mechanisms until a large perturbation drives a state change (Scheffer et al., 2001). The conceptual model also illustrates potential mechanisms that promote woody persistence once *Baccharis* successfully invades a grassland site. Progressive effects of woody encroachment on soil moisture availability, understory biomass, herbivory on woody seedlings (Hobbs and Mooney, 1986), and fine litter accumulations may all contribute to maintaining woody dominance and allowing it to spread into nearby grassland sites. Below, we discuss these potential links among progressive ecosystem changes following woody encroachment.

4.1. Ecosystem response

Net increases in biomass and tissue and soil C:N contributed to increases in total ecosystem carbon storage of over 125% from uninvaded grassland to sites occupied by

Baccharis for 25 years. This is surely an underestimate because it excludes all C storage at soil depths >0.5 m. The observed increases in carbon storage also did not appear to be saturating at 25 years after shrub establishment in any pool, suggesting the potential for additional carbon gains beyond 25 years. If this is the case, a relatively small increase in *Baccharis* encroachment rates could produce important changes in ecosystem carbon storage at the landscape scale.

Two annual grasslands near our study site exposed to 6 years of elevated CO₂ showed little or no increase in ecosystem C storage despite modest increases in NPP. While multi-year global change studies have detected only modest, transient responses of soil C at sites including Jasper Ridge (Hungate et al., 1996, 1997; Körner, 2000), our findings support the concept that large changes in C stocks may be driven indirectly by vegetation responses to global changes on longer time-scales (Bachelet et al., 2001). Modeling and observational studies in the deserts of the southwestern US, another region experiencing accelerated woody encroachment, identified important increases in soil and plant C stocks accompanying the replacement of grasslands by woody vegetation (Asner et al., 2003; Hibbard et al., 2003). However, other work indicates that increases in C stocks with woody encroachment might occur only in drier regions, with grassland-to-woodland transitions in some wetter areas actually yielding net soil C losses (Jackson et al., 2002). Accurate estimates of the net C storage effect of woody encroachment on a regional to global scale therefore will likely require data from additional studies in a range of locations.

We initially hypothesized that *Baccharis*-invaded sites would experience increasing N limitation as N was immobilized in biomass and litter. However, total soil N increased rapidly with shrub age. Moreover, the magnitude of increase in total soil nitrogen was much larger than the increase in nitrogen immobilization in biomass and litter over time. Concentrated use of *Baccharis* by animals for cover and forage (McBride and Heady, 1968; Bartholomew, 1970; Hobbs and Mooney, 1986) might transport nitrogen to shrub understories from surrounding areas, providing a new source of N. It is also possible that root transport of soil nitrogen from deeper soils or surrounding areas and differences in soil erosion and rainsplash between shrub and grassland areas each may contribute to increased soil N under shrubs. Root transport of N from shallow soils underlying nearby grassland areas would likely reduce nearby grassland productivity. Biomass production values at our 15 grassland sites were comparable to values at a range of unfertilized and fertilized sites nearby (Zavaleta, 2001), suggesting that there was no significant shrub removal of N from grassland sites 4 m from shrubs. Quantification of soil inorganic N and mineralization rates is necessary to confirm the effects of *Baccharis* encroachment on plant-available soil nitrogen.

Declines in herbaceous understory production and in the contribution of *Baccharis* to ANPP with shrub age occurred in spite of increasing soil N and soil moisture, key limiting resources in this ecosystem. In previous studies, reduced herbaceous ANPP beneath and near *Baccharis* and other canopies was found to be driven largely by increased herbivory (Bartholomew, 1970; Hobbs and Mooney, 1986). Herbaceous ANPP may also have declined due to decreased light levels in the understory (McBride and Heady, 1968). The sharp decline in *Baccharis* ANPP after 20 years may reflect natural senescence (Hobbs and Mooney, 1986) as well as increased competition from establishing oaks and other woody species.

In grasslands at Jasper Ridge Preserve, rooting is heavily concentrated in the top 15 cm of soil (B. Shaw, unpubl. data). Shrub establishment appears to replace some of this

shallow root biomass rather than increase it. The rise and subsequent decline of root biomass in the 15–30 cm depth interval mirrors the trend in live above-ground shrub biomass through time, suggesting that *Baccharis* itself dominated rooting in this depth interval. As *Baccharis* senesces above-ground, reducing both C fixation and demand for water and nutrients, root biomass may also decline. Steady increases in roots at 30–47 cm depth over the 25-year chronosequence might therefore reflect the establishment of more deeply rooted *Quercus* in the *Baccharis* canopy rather than continued growth of *Baccharis* roots.

4.2. Species composition and succession

Previous studies have shown that shrubs including *Baccharis* can serve as nurse plants for young oaks in California grassland–woodland landscapes, promoting succession to oak woodland (McBride and Heady, 1968; Callaway and D’Antonio, 1991; Callaway, 1992; Callaway and Davis, 1993, 1998). However, most other studies have not controlled for nurse shrub age and have not been able to rule out the possibility that more oaks established under shrubs than in open grassland simply because the same micro-site characteristics that permitted shrub establishment also favored oaks (but see Callaway, 1992). Our results support the hypothesis that shrubs, not the sites they invade, benefit oak recruitment. We found oaks only under *Baccharis* at least 15-years old. If *Baccharis*-invaded sites were inherently favorable to oaks, we would have found oaks at shrub sites of all ages. The finding that oaks establish only under mature shrubs strongly suggests that features of mature shrubs—and their effects on site characteristics—benefit establishing oaks.

Various other studies have suggested that increased moisture, moderated temperature, reduced herbaceous biomass, protection of oak seedlings and acorns from herbivory, and attraction of acorn dispersers might all contribute to shrub facilitation of oak establishment in California grassland–woodland systems (McBride and Heady, 1968; Callaway and D’Antonio, 1991; Callaway, 1992; Callaway and Davis, 1993, 1998). Our results support some of these mechanisms. Progressive declines with shrub age in herbaceous understory biomass might have increased the probability of successful oak recruitment under older shrubs. Herbaceous biomass and competition from grasses strongly influence the establishment of woody plants in grassland (Knoop and Walker, 1985; Brown and Archer, 1989; Hughes and Vitousek, 1993; Martinez and Fuentes, 1993; Eliason and Allen, 1997), including *Baccharis* (DaSilva and Bartolome, 1984). Competition with herbaceous vegetation for moisture affected growth and establishment of blue oaks in California grassland (Gordon et al., 1989) and of bur and pin oak (*Q. macrocarpa* and *Q. ellipsoidalis*) in a Minnesota old field (Davis et al., 1999). An additional mechanism favoring oak establishment under mature but not young shrub canopies might be the replacement of fine herbaceous litter with woody litter. Acorns require contact with mineral soil to germinate (Borchert et al., 1989) and might be more likely to reach mineral soil at sites with both reduced herbaceous biomass and fine litter loads.

Soil moisture is also a critical factor to woody establishment in a variety of grassland and desert systems (Archer et al., 1988; Turner, 1990; Harrington, 1991; O’Connor, 1995; Reid and Ellis, 1995; Brown et al., 1997) and is crucial to *Baccharis* establishment in this grassland (DaSilva and Bartolome, 1984; Williams et al., 1987; Williams and Hobbs, 1989; Zavaleta, 2001). Soil moisture availability strongly influences the growth of blue oak

(*Q. douglasii*) seedlings (Gordon and Rice, 2000), and drought appeared responsible for most *Q. agrifolia* seedling mortality in a study in open grassland (Callaway and D'Antonio, 1991). If soil moisture increased through a portion of the spring with *Baccharis* age, as suggested by our April soil moisture samples, it might increase the probability of successful oak germination and establishment under only older shrubs.

Native California grasses and forbs are thought to be poor competitors against the Mediterranean exotic annuals that now dominate California annual grasslands. Previous work in a California coastal grassland similar to our study site shows that biomass clipping, which reduces the dominant exotic vegetation, enhances growth, fitness, and recruitment of native annuals (G. Hayes, unpubl. data). The increase in relative native biomass and decline in total exotic biomass that we observed in the understory over time may reflect the advantage that native grasses have over exotics as biomass reduction by herbivores increases. Enhancement of both native relative biomass in the understory and succession to long-lived native oaks by maturing shrubs indicates that *Baccharis* encroachment may have community restoration and conservation implications as well as impacts on ecosystem functioning.

5. Conclusions

While many climate models now incorporate the effects of short-term energy and resource exchanges between the atmosphere and the biosphere, most do not consider feedbacks associated with long-term vegetation changes (Foley et al., 2000). Global change experiments have successfully captured the onset of community change but not its long-term implications for ecosystem function (Chapin et al., 1995; Harte and Shaw, 1995; Grime et al., 2000). Multi-year studies in natural systems with short generation times, such as annual grasslands, can be powerful tools for exploring the mechanisms of community-mediated effects on ecosystem function (Potvin and Vasseur, 1997; Leadley et al., 1999). However, only in combination with other experimental and modeling approaches can they provide information about the long-term ecosystem effects of key shifts in plant species composition, such as invasion of an annual community by one or more dominant perennial species.

Coupled with recent evidence that recruitment of *Baccharis* in California grasslands may increase under future climate changes (Zavaleta, 2001), our findings illustrate the potential for important vegetation-mediated ecosystem responses and feedbacks to atmospheric CO₂ and climate change. Many of the changes we observed were progressive and did not saturate with time since woody encroachment, illustrating that the long-term ecosystem consequences of a single invader can be much greater than estimated from short-term observations following establishment. The changes that we observed in variables such as productivity and C storage were both larger and more sustained than changes observed in multi-year studies of ecosystem responses to future climate and atmospheric changes. Vegetation-mediated effects are therefore likely to play a major role in the influences of anthropogenic climate and atmospheric change on functioning in some ecosystems. Additional studies scaling from multi-year, plot-scale experiments to decadal dynamics on whole landscapes will strengthen understanding of these links and expand important connections between empirical field studies and global models of vegetation and biogeochemical response to anthropogenic change.

Acknowledgments

We thank Chris Field, Peter Vitousek, and Pamela Matson for guidance and support throughout this project. Phillippe Cohen, Nona Chiariello, Gordon Holtgrieve, Rebecca Young and the Jasper Ridge Biological Preserve provided valuable logistical support. ESZ was supported by a US Environmental Protection Agency STAR Fellowship and by the A. W. Mellon Foundation.

References

- Archer, S., Scifres, C., Bassham, C.R., 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58, 111–127.
- Asner, G.P., Archer, S., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. *Global Change Biology* 9, 316–335.
- Bachelet, D., Neilson, R.P., Lenihan, J.M., Drapek, R.J., 2001. Climate change effects on vegetation distribution and carbon budget in the United States. *Ecosystems* 4, 164–185.
- Bartholomew, B., 1970. Bare zone between California shrub and grassland communities, the role of animals. *Science* 170, 1210–1212.
- Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., Mwonga, S.M., 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* 26, 1005–1024.
- Borchert, M.I., Davis, F.W., Michaelsen, J., Oyler, L.D., 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70, 389–404.
- Bormann, B.T., Spaltenstein, H., McClellan, M.H., Ugolini, F.C., Cromack, K., Nay, S.M., 1995. Rapid soil development after windthrow disturbance in Pristine Forests. *Journal of Ecology* 83, 747–757.
- Brown, J.R., Archer, S., 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80, 19–26.
- Brown, J.R., Carter, J., 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* 13, 93–102.
- Brown, J.H., Valone, T.J., Curtin, C.G., 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Sciences* 94, 9729–9733.
- Calder, J.A., Wilson, J.B., Mark, A.F., Ward, G., 1992. Fire, succession, and reserve management in a New Zealand snow tussock grassland. *Biological Conservation* 62, 35–45.
- Callaway, R.M., 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73, 2118–2128.
- Callaway, R.M., D'Antonio, C.M., 1991. Shrub facilitation of coast live oak establishment in central California. *Madrono* 38, 158.
- Callaway, R.M., Davis, F.W., 1993. Vegetation dynamics, fire, and the physical-environment in coastal central California. *Ecology* 74, 1567–1578.
- Callaway, R.M., Davis, F.W., 1998. Recruitment of *Quercus agrifolia* in central California: the importance of shrub-dominated patches. *Journal of Vegetation Science* 9, 647–656.
- Carreira, J.A., Niell, F.X., Lajtha, K., 1994. Soil-nitrogen availability and nitrification in Mediterranean Shrublands of varying fire history and successional stage. *Biogeochemistry* 26, 189–209.
- Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Laundre, J.A., 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76, 694–711.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Sala, O.E., Reynolds, H.L., Hooper, D.U., Mack, M., Diaz, S.E., Hobbie, S.E., Lavorel, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- DaSilva, P.G., Bartolome, J.W., 1984. Interaction between a shrub, *Baccharis pilularis* subsp. *consanguinea* (Asteraceae), and an annual grass, *Bromus mollis* (Poaceae), in coastal California. *Madrono* 31, 93–101.
- Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T., Muermann, C., 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecology* 145, 341–350.

- Diaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science* 8, 463–474.
- Diaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* 16, 646–655.
- Eliason, S.A., Allen, E.B., 1997. Exotic grass competition in suppressing native shrubland re-establishment. *Restoration Ecology* 5, 245–255.
- Fastie, C.L., 1995. Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay; Alaska. *Ecology* 76, 1899–1916.
- Foley, J.A., Levis, S., Costa, M.H., Cramer, W., Pollard, D., 2000. Incorporating dynamic vegetation cover with global climate models. *Ecological Applications* 10, 1620–1632.
- Gordon, D.R., Rice, K.J., 2000. Competitive suppression of *Quercus douglasii* (Fagaceae) seedling emergence and growth. *American Journal of Botany* 87, 986–994.
- Gordon, D.R., Welker, J.M., Menke, J.W., Rice, K.J., 1989. Competition for soil water between annual plants and blue oak seedlings. *Oecologia* 79, 533–541.
- Grime, J.P., Brown, V.K., Thompson, K., Masters, G.J., Hillier, S.H., Clarke, I.P., Askew, A.P., Corker, D., Kielty, J.P., 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* 289, 762–765.
- Harrington, G.N., 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* 72, 1138–1149.
- Harte, J., Shaw, R., 1995. Shifting dominance within a montane vegetation community: results of a climate warming experiment. *Science* 267, 876–880.
- Hibbard, K.A., Schimel, D.S., Archer, S., Ojima, D.S., Parton, W., 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. *Ecological Applications* 13, 911–926.
- Hobbs, R.J., Mooney, H.A., 1986. Community changes following shrub invasion of grassland. *Oecologia* 70, 508–513.
- Houghton, J.T., Filho, L.G.M., Callander, B., Kattenburg, A., 1996. *Climate Change 1995: The Science of Climate Change*. Cambridge University Press, Cambridge 572pp.
- Hughes, F., Vitousek, P.M., 1993. Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawai'i. *Oecologia* 93, 557–563.
- Hungate, B.A., Jackson, R.B., Field, C.B., III, F.S.C., 1996. Detecting changes in soil carbon in CO₂ enrichment experiments. *Plant and Soil* 187, 135–145.
- Hungate, B.A., Holland, E.A., Jackson, R.B., III, F.S.C., Mooney, H.A., Field, C.B., 1997. The fate of carbon in grasslands under carbon dioxide enrichment. *Nature* 388, 576–579.
- Jackson, R.B., Banner, J.L., Jobbagy, E.G., Pockman, W.T., Wall, D.H., 2002. Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418, 623–626.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Knoop, W.T., Walker, B.H., 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73, 235–253.
- Leadley, P.W., Niklaus, P.A., Stocker, R., Korner, C., 1999. A field study of the effects of elevated CO₂ on plant biomass and community structure in a calcareous grassland. *Oecologia* 118, 39–49.
- Lichter, J., 1998. Primary succession and forest development on coastal Lake Michigan sand dunes. *Ecological Monographs* 98, 487–510.
- Martinez, E., Fuentes, E., 1993. Can we extrapolate the California model of grassland–shrubland ecotone? *Ecological Applications* 3, 417–423.
- McBride, J.R., 1974. Plant succession in the Berkeley Hills, California. *Madrono* 22, 317–380.
- McBride, J., Heady, H.F., 1968. Invasion of a grassland by *Baccharis pilularis* DC. *Journal of Range Management* 21, 106–108.
- Nielson, R.P., 1986. High-resolution climatic analysis and southwest biogeography. *Science* 232, 27–34.
- Norland, E.R., Hix, D.M., 1996. Composition and structure of a chronosequence of young, mixed-species forests in southeastern Ohio, USA. *Vegetatio* 125, 11–30.
- O'Connor, T.G., 1995. *Acacia karroo* invasion of grassland: environmental and biotic effects influencing seedling emergence and establishment. *Oecologia* 103, 214–233.
- Pacala, S., Hurtt, G.C., Houghton, R.A., Birdsey, R.A., Heath, L., Sundquist, E.T., Stallard, R.F., Baker, D., Peylin, P., Ciais, P., Moorcroft, P., Caspersen, J., Shevliakova, E., Moore, B., Kohlmaier, G., Holland, E.,

- Gloor, M., Harmon, M.E., Fan, S.M., Sarmiento, J.L., Goodale, C., Schimel, D., Field, C.B., 2001. Convergence of land- and atmosphere-based US carbon sink estimates. *Science* 292, 2316–2320.
- Pardo, L.H., Driscoll, C.T., Likens, G.E., 1995. Patterns of nitrate loss from a chronosequence of clear-cut watersheds. *Water Air and Soil Pollution* 85, 1659–1664.
- Polley, H.W., Mayeux, H.S., Tischler, C.R., 1996. Are some of the recent changes in grassland communities a response to rising CO₂ concentrations? In: Korner, C., Bazzaz, F.A. (Eds.), *Carbon Dioxide, Populations, and Communities*. Academic Press, San Diego, pp. 177–195.
- Potvin, C., Vasseur, L., 1997. Long-term CO₂ enrichment of a pasture community: species richness, dominance, and succession. *Ecology* 78, 666–677.
- Ranger, J., Marques, R., Colinbelgrand, M., Flammang, N., Gelhaye, D., 1995. The dynamics of biomass and nutrient accumulation in a douglas-fir (*pseudotsuga-menziessii* Franco) stand studied using a chronosequence approach. *Forest Ecology and Management* 72, 167–183.
- Reid, R.S., Ellis, J.E., 1995. Impacts of pastoralists on woodlands in South Turkana, Kenya: livestock-mediated tree recruitment. *Ecological Applications* 5, 978–992.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Schimel, D., Melillo, J., Tian, H., McGuire, A.D., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S., Thornton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO₂ and climate to carbon storage by ecosystems in the United States. *Science* 287, 2004–2006.
- Schlesinger, W.H., Pilmanis, A.M., 1998. Plant–soil interactions in deserts. *Biogeochemistry* 42, 169–187.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A., Whitford, W.G., 1990. Biological feedbacks in global desertification. *Science* 247, 1043–1048.
- Tabachnick, B.G., Fidell, L.S., 1996. *Using Multivariate Statistics*. HarperCollins College Publishers, New York.
- Turner, R.M., 1990. Long-term vegetation change at a fully protected Sonoran desert site. *Ecology* 71, 464–477.
- Uriarte, M., 2000. Interactions between goldenrod (*Solidago altissima* L.) and its insect herbivore (*Trirhabda virgata*) over the course of succession. *Oecologia* 122, 521–528.
- Vitousek, P.M., Farrington, H., 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. *Biogeochemistry* 37, 63–75.
- Williams, K., Hobbs, R.J., 1989. Control of shrub establishment by spring time soil water availability in an annual grassland. *Oecologia* 81, 62–66.
- Williams, K., Hobbs, R.J., Hamburg, S.P., 1987. Invasion of an annual grassland in Northern California by *Baccharis pilularis* spp. *consanguinea*. *Oecologia* 72, 461–465.
- Wilson, J.B., Agnew, A.D.Q., 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23, 263–336.
- Zar, J.H., 1996. *Biostatistical Analysis*. Prentice-Hall, Upper Saddle River, NJ.
- Zarin, D.J., Johnson, A.H., 1995. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Science Society of America Journal* 59, 1444–1452.
- Zavaleta, E.S., 2001. *Influences of Climate and Atmospheric Changes on Plant Diversity and Ecosystem Function in a California Grassland*. Department of Biological Sciences, Stanford University, Stanford, 138pp.