

Vegetation Change and the Role of Atmospheric CO₂ Enrichment on a Relict Site in Central Oregon: 1960-1994

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Abstract:

Atmospheric CO₂ enrichment is increasingly implicated as a contributory cause of vegetation change on North American rangelands. To explore the role of the rising CO₂ content of the earth's atmosphere as an agent of vegetation change, we revisited (June 1994) the Island Research Natural Area (IRNA), a relict site of semiarid vegetation in central Oregon, to conduct a replicate survey of Driscoll's (1962) 1960 work. IRNA is one of the best non-laboratory settings to examine CO₂-induced vegetation change because human activities have been limited there. The physiological effects of increased levels of atmospheric CO₂ include increased photosynthetic rates, reduced transpiration rates, and increased water-use efficiency. While all species benefit from atmospheric CO₂ enrichment, the increase in CO₂ alters competitive interactions, typically favoring those species that outcompete others for light, nutrients, habitat, and other resources necessary for reproductive success.

Our results show that between 1960 and 1994 IRNA experienced large increases in woody-species cover and density, no change in perennial herbaceous cover, and decreases in annual cover. Western juniper density and cover increased by 41 percent and 113 percent, respectively. Similarly, big sagebrush density and cover approximately doubled. These findings are similar to findings reported in other long-term studies conducted at sites with a variety of land-use activities. We found, however, that none of the traditional mechanisms typically invoked to explain these changes were compatible with the biotic changes that we observed. On the IRNA site, no organized fire suppression had occurred, grazing had been absent since the 1920s, logging was non-existent, variabilities in seasonal water-year precipitation totals were not statistically significant between the 2-, 10-, and 34-year periods prior to each vegetation survey, and disease or pest infestation was not evident. We conclude that the vegetation changes observed are consistent with laboratory and controlled field experiments that enrich the air with CO₂.

Key Words: CO₂ enrichment, central Oregon, sagebrush-steppe, vegetation change.

Article:

An emerging paradigm in ecological studies challenges the concepts of ecosystem stability and ecological balance of plant communities. Johnson and Mayeux (1992) argue that the species-constant climax theory is incorrect because of the rarity of stable plant assemblages. Change in vegetation composition and dominance should be viewed not as unusual or unnatural, but as a normal component of ecosystem dynamics. That said, the rate and direction of vegetation change are important, especially if changes are enhanced by anthropogenic processes such as elevated levels of atmospheric CO₂ resulting from de-forestation and the combustion of fossil fuels. The purpose of this research is to determine if atmospheric CO₂ enrichment has been a contributory cause of vegetation change on a relict area in central Oregon.

The role of humans in altering vegetation communities in the arid and semiarid range-lands of the American West has been, and likely will continue to be, significant (Webb et al. 1987; Knapp 1991; 1992). Numerous studies (e.g., Hastings and Turner 1965; Rogers 1982; Bahre 1991; Veblen and Lorenz 1991) chronicle historic

vegetation changes in the American West following occupation by settlers of European descent. These studies attribute vegetation change to four broad causes: changes in fire regimes, changes in grazing intensities, cyclic trends in climate, and extensive logging. While all of these factors have influenced various vegetation associations within the West, substantial evidence suggests an additional cause for vegetation change.

In an extensive literature review of traditional vegetation change mechanisms, Mayeux et al. (1991:65) stated that "no compelling evidence exists which substantiates that any single one or combination of them [factors] is responsible." In support of this view, changes in rangeland vegetation on a global scale appear to be occurring regardless of land-stewardship practices (Mayeux et al. 1991). For example, in the big sagebrush-dominated (*Artemisia tridentata* Nutt.) vegetation of the southern Great Basin Desert, Hunter (1991) documented substantial increases in cheatgrass (*Bromus tectorum* L.) cover and frequency on the Nevada Test Site since the 1960s and in the absence of human activities. In a study of a western juniper (*Juniperus occidentalis* Hook) stand in north-eastern California, Young and Evans (1981) determined that none of the common hypotheses (i.e., fire, grazing, and climatic shifts) adequately explained juniper invasion into big sagebrush communities. LaMarche et al. (1984), Graybill (1987), and Graybill and Idso (1993) showed that growth patterns in bristlecone pine (*Pinus longaeva* D. K. Bailey) and limber pine (*P. flexilis* James) at sites above 3100 m in the American West over the past 200 years vastly exceeded growth rates typical of the preceding millennium. The rapidly rising growth rates of these trees, they concluded, may be a function of rising CO₂ content in the atmosphere over the same period. Finally, several researchers (e.g., Hays 1991; Idso 1992; Johnson et al. 1993) have suggested that the worldwide invasion of grasslands by trees and shrubs is consistent with results of laboratory studies of plants exposed to atmospheric CO₂ enrichment.

One theory advanced to explain vegetation change in the absence of either significant anthropogenic or climatic variations rests on empirical observations of differential (but positive) plant responses to increases in atmospheric CO₂ concentrations (Idso 1989). The principal physiological effects of aerial CO₂ fertilization are enhanced photosynthetic rates coupled with reduced transpiration rates for most species (Rozema 1993; Garcia et al. 1994). Kimball's (1983:779) review of 437 observations of 37 species exposed to a doubling of atmospheric CO₂ (from 330 ppm to 660 ppm) indicated that agricultural yield increased by approximately 33 percent. Similarly, Kimball and Idso (1983:61), analyzing results from 46 experiments with 18 different crop species exposed to CO₂ doubling, determined that mean transpiration rates were lowered by approximately 34 percent. Plants that grow in CO₂ enriched environments, moreover, tend to be larger and taller, have more and thicker leaves, more branches or tillers, and greater root systems than similar plants growing under ambient (normal CO₂) conditions (Idso 1989).

Given CO₂'s potential as a causative factor of rangeland vegetation change, we returned to the Island Research Natural Area (IRNA), a relict sagebrush-steppe vegetation association in semiarid central Oregon, and replicated Driscoll's 1960 vegetation survey (1962; 1964). As a site for a repeat study, this one is ideal since it represents one of the few minimally disturbed sagebrush-steppe environments of the United States. Specifically, we compared vegetation changes over a 34-year period and analyzed the "fit" of these changes with expected changes in plant growth attributable to increases in atmospheric CO₂ concentration (i.e., greater foliage production and increased water-use efficiency (Δ WUE)) (Kimball and Idso 1983; Garcia et al. 1994). These atmospheric changes should favor a shift toward greater dominance of woody species for four reasons: first, an increase in WUE favors the expansion of woody species previously held in check by insufficient precipitation (Idso 1989); second, these woody species typically produce greater foliage than competing non-woody species, thereby outcompeting them for light (Johnson et al. 1993); third, as Idso and Kimball (1993) have shown, trees are considerably more responsive than non-woody plants to atmospheric CO₂ enrichment; and fourth, as Johnson et al. (1993) have noted, these effects on woody species should be subject to the "compound interest law of plant growth" (Blackman 1919:353) whereby the differences between those species that benefit the most and those that benefit the least widens with time.

Our study addresses three specific questions. First, how did vegetation composition, cover, and density at the IRNA change from 1960 to 1994? Second, if changes did occur, were these changes consistent with what would

be expected as a result of CO₂ aerial fertilization? Third, are these vegetation changes a function of multiple factors working in concert (i.e., fire, climatic variability, grazing, pathogens) or, in the absence of these, of CO₂ enrichment? Answers to these questions may help shed light on the current debate over the indirect effects of human activities (such as CO₂ enrichment) on native vegetation communities—especially in a semiarid environment that is particularly sensitive to this type of change.

Consequences of CO₂ Enrichment on Plant Growth

Increased water-use efficiency (the ratio of photosynthesis to transpiration) is one of the major consequences of CO₂ enrichment (Mayeux et al. 1991). Polley et al. (1993) estimate that WUE may have increased approximately 27 percent in C₃ plants during the last 200 years as a result of decreased transpiration (because of decreases in stomatal conductance), increased assimilation, and the combination of the two (Eamus 1991). Idso (1989) found that doubling atmospheric CO₂ led to a doubling of WUE, and that this result was consistent among different species. Given that current atmospheric CO₂ concentrations are approximately 360 ppmv (Figure 1; Keeling and Whorf 1994), some scholars (Mayeux et al. 1991) believe that increases in atmospheric CO₂ are a viable cause for rangeland vegetation changes. Worldwide, the increases in CO₂ in the last century have been particularly dramatic, rising from approximately 296 ppmv in 1899 (Neftel et al. 1994) to 317 ppmv in 1960 (Figure 1; Keeling and Whorf 1994). The rise to 360 ppv between 1960 to 1994 alone represents a 14 percent increase.

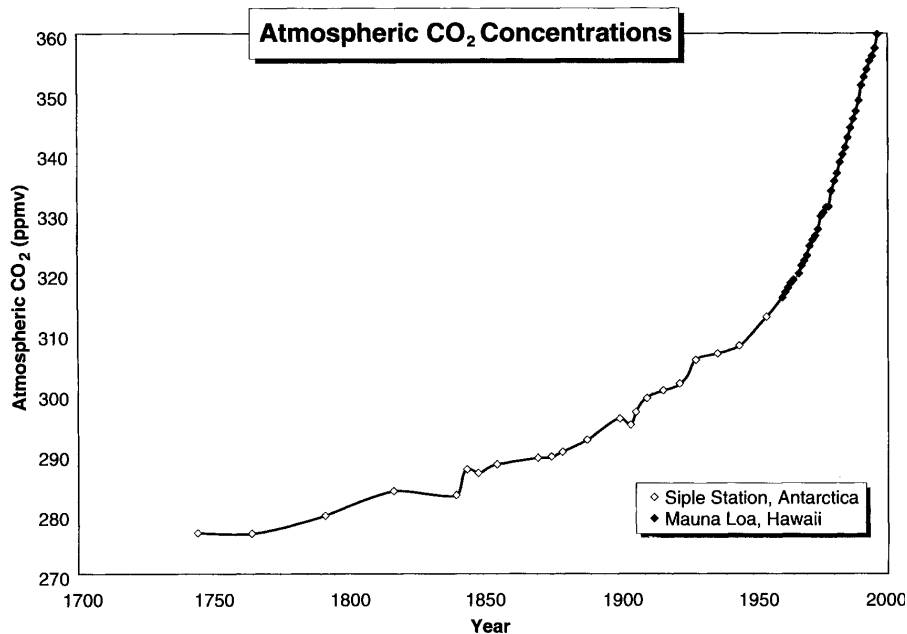


Figure 1. Atmospheric carbon dioxide concentrations from 1744 to present. Data prior to 1959 (open diamonds) are from Siple Station, Antarctica Ice Cores (Neftel et al. 1994), while post-1958 data (solid diamonds) are from Mauna Loa, Hawaii air samples (Keeling and Whorf 1994).

Most research concerning the effects of CO₂ enrichment has been conducted in laboratory settings, and it is unclear whether results from these studies can be extrapolated into natural environments (Mayeux et al. 1993; Mooney et al. 1991). The primary problem is that it is difficult to separate human impacts from natural environmental influences on plant growth. Moreover, other factors that may influence plant growth, such as soil nutrient status, may differ substantially between controlled laboratory experiments and natural environments. Finally, the duration of these studies is often short, with observations ranging from days (e.g., Sionit and Patterson 1984) to months (e.g., Sage et al. 1989) to a few years (e.g., Surano et al. 1986; Bazzaz et al. 1993), although the sour orange tree study of Idso and Kimball (1993) will soon have spanned a full decade.

Studies of elevated atmospheric CO₂ concentrations and native plant communities have been conducted on a Chesapeake Bay coast salt marsh (Curtis et al. 1989a; 1989b; 1990; Drake and Leadly 1991) and Arctic tussock tundra (Oechel and Riechers 1986; Tissue and Oechel 1987). In these studies, the marsh ecosystem largely responded positively to increased CO₂ while the Arctic tundra generally did not. The latter's ecosystem response appears to be limited because the benefits of elevated CO₂ concentrations are muted by consistently low

temperatures (Idso 1989) and the frozen soil that makes most nutrients inaccessible (Tissue and Oechel 1987). Regrettably, field studies have not been conducted in natural ecosystems where the effects of CO₂ enrichment are most likely to be expressed—arid and semiarid rangelands (Mooney et al. 1991; Mayeux et al. 1994).

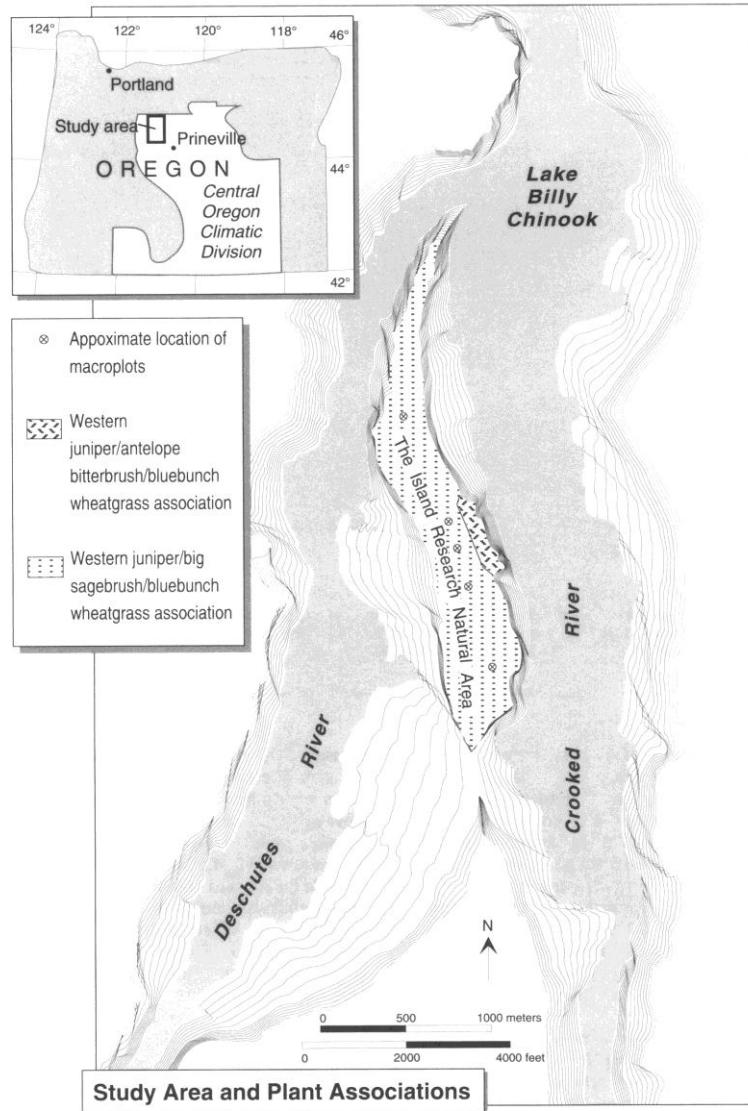


Figure 2. Location of The Island Natural Research Area, boundaries of the vegetation associations, and approximate location of the macroplots.

Study Area

The Island Research Natural Area (IRNA), a relict area in semiarid central Oregon at 44° 34' N, 121° 16' W (Figure 2), is under the management of the Prineville, Oregon Bureau of Land Management (BLM) District and the Crooked River National Grasslands. Classified an "Area of Critical Environmental Concern/ Research Natural Area" (Figure 2; Halvorson 1991), IRNA has been free of grazing and other direct human influences for nearly 70 years. Direct human impacts to IRNA, other than people examining the area, have been confined to two successive summers of grazing by domestic sheep in the 1920s (Halvorson 1991; Driscoll 1995). IRNA occupies 78 ha of basaltic plateau at the confluence of the Crooked and Deschutes Rivers and is hemmed, with the exception of the south slope, by 60 to 215 m vertical cliffs (Driscoll 1964). Access is restricted to a steep, crude trail on the southwest slope. Thus, human use is limited.

IRNA's climate is semiarid with winter precipitation (primarily snow) accounting for over half the annual total of 25 cm. Temperatures at nearby Prineville show strong continentality with July and January means of 18.1°C and -0.4°C, respectively (Karl et al. 1990).

IRNA contains two distinct vegetation associations: 1) the western juniper/big sagebrush/ bluebunch wheatgrass

association (*Juniperus occidentalis*/*Artemisia tridentata* Nutt./*Agropyron spicatum* Pursh) occupying approximately 67 ha; and 2) the western juniper/antelope bitterbrush/bluebunch wheatgrass association (*J. occidentalis*/*Purshia tridentata* Pursh/*Agropyron spicatum*) occupying approximately 11 ha (Figures 2, 3, and 4; Driscoll 1964). Other common species are Sandberg bluegrass (*Poa secunda* Vasey) and Thurber's needlegrass (*Stipa thurberiana* Piper). A 1960 and 1961 inventory of vegetation composition, cover, and constancy (Driscoll 1964) identified 22 species (other species located on the site were either vernal and unidentifiable or scarce). Soils on the juniper/sagebrush/wheatgrass association are two types of Brown loams comprised of different parent materials, one from lake-laid sediments, the other from loess and very fine sands (Driscoll 1962). Soil chemistry values range between pH 6.5 to pH 7.0 (Driscoll 1964). Soil on the juniper/bitterbrush/wheat-grass association is classified as a sandy loam Regosol of aeolian origin with surface pH values ranging from 6.0 to 6.5 (Driscoll 1964). Vegetation is grazed by native herbivores and granivores, including Rocky Mountain mule deer (*Odocoileus hemionus*), cottontail rabbits (*Sylvilagus nutalli*), western harvester ants (*Pogonomyrmex owyheei*), mice (*Microtus* sp.), chipmunks (*Eutamias* sp.), and ground squirrels (*Citellus* sp.) (Driscoll 1964; personal observations 1994). Clearings by western harvester ants are abundant throughout IRNA, while the grazing impacts of mule deer are modest, probably because of the lack of a water source.

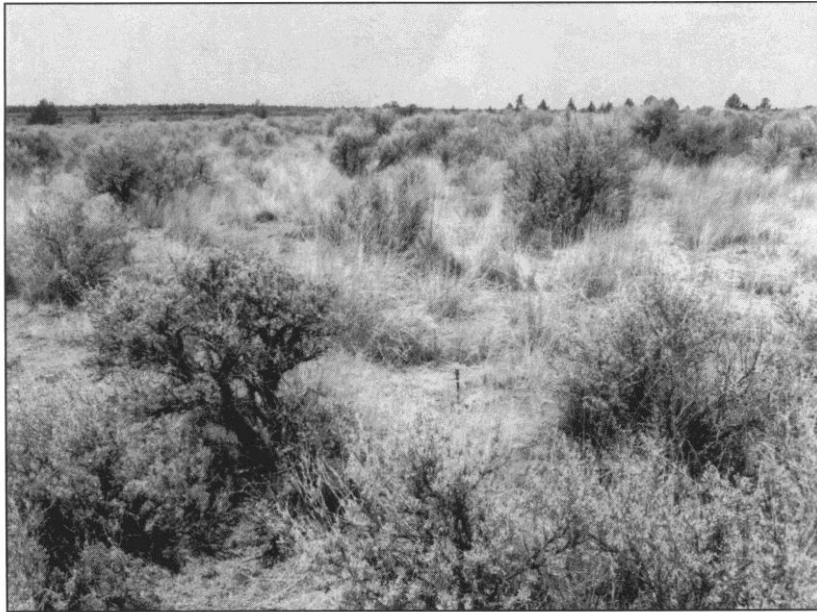


Figure 3. Big sagebrush and bunchgrasses. Typical cover and density on macroplot #5 at IRNA. Photograph by authors.

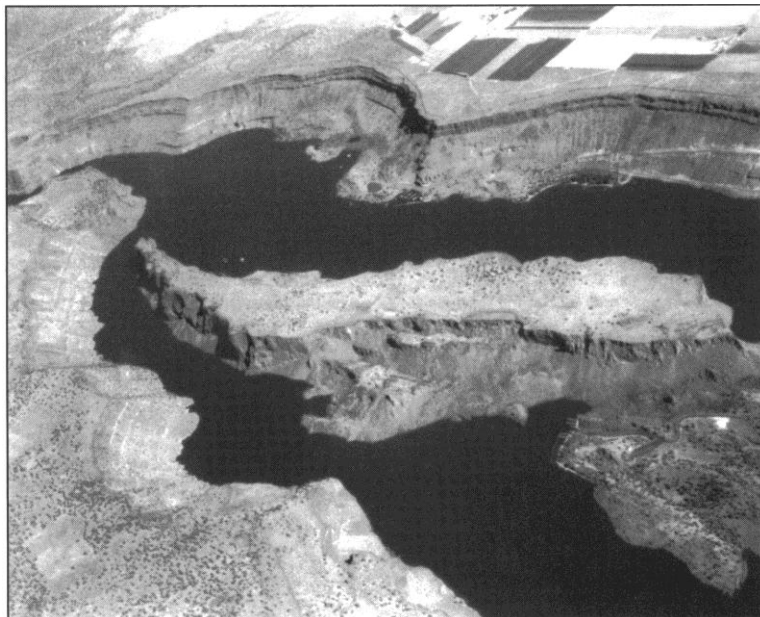


Figure 4. Aerial photograph of IRNA looking east. Lake Billy Chinook surrounds all but the south end of IRNA. October 1994. Photograph by Thom Martin.

Data and Methods

Driscoll's Benchmark Data:

Driscoll (1962; 1964) measured five components of vegetation: 1) individual species foliage cover; 2) basal area and total foliage cover of perennial herbs; 3) foliage cover of shrubby and suffrutescent species; 4) maximum average height of mature shrubby and suffrutescent species; and 5) densities of shrubby and suffrutescent species.

Driscoll (1962; 1964) examined vegetation on five 15.25 × 30.5 m (50 × 100') permanent macroplots within the *Juniperus/Artemisia/Agropyron* vegetation association of IRNA during July and August of 1960. Within each macroplot, four 15.25 m line transects were set in restricted random fashion and marked with rebar stakes. Ten observation plots of 0.3 × 0.6 m (1' × 2') were systematically placed along each transect and the percentage of herbaceous species foliage cover and the basal areas of perennial herbaceous species were estimated by eye. While ocular estimation lends itself to considerable subjectivity, Driscoll (1994) minimized subjectivity by placing concentric rings (representing 2 percent, 5 percent, and 10 percent of the area of the observation plots) on the vegetation to ensure more consistent measurements. He measured shrub cover where the 15.25 m line transects intercepted the shrubs; shrub density (by species) on each macroplot by counting the number of individuals located within a 1.22 m (4') belt transect that bisected the line transect (total area per macroplot: 37.2 m² (400 ft²); average maximum height of adult shrubs (by species) by measuring those within the belt transects; and percentage cover of western juniper for the entire IRNA by measurements from aerial photographs (Driscoll 1962; 1964).

Comparison of Data: 1960-1994

Using methods identical to Driscoll's, we replicated his vegetation survey (with the exception of the juniper survey) in late June, 1994. We located all five of Driscoll's macroplots and 15 of his 20 rebar-marked transects within them. The five transects we could not find were located randomly within the macroplots. This does not invalidate our comparisons because of the consistency of vegetation within the macroplots (this was part of Driscoll's selection criteria). The data for 1960 and 1994 were compared using difference-of-means tests. In the case of our western juniper survey, we analyzed aerial photos of IRNA taken in 1961, 1979, 1985, and 1994. Percentage cover and density values of western junipers were based on mean values of three sample counts for each photograph. Counting the number of trees on IRNA yielded tree density. Percentage tree cover was determined by placing a dot-grid transparency overlay (25 dots per 1.25 cm², 0.2 cm apart) on the photographs. Dots intersecting junipers in relation to the total number of dots intersecting IRNA were then counted and converted into a percentage (Lillesand and Kiefer 1994).

Results

Shrub, Tree, and Herbaceous Cover

Vegetation change on IRNA over the last 34 years is characterized by large increases in woody species, modest change in perennial grasses, and a reduction in annuals (Table 1). While the total number of species with measurable cover decreased from 16 in 1960 to 12 in 1994, we found that total perennial cover increased by 11 percent—from 28 percent in 1960 to 39 percent in 1994 (a relative increase of 39 percent over 1960 values). While big sagebrush and bluebunch wheatgrass provided the greatest cover in both 1960 and 1994, their relative importance switched during the 34-year period. Big sagebrush increased significantly from 1960 to 1994 (nearly doubling from 8.5 to 15.6 percent). Rubber rabbitbrush (*Chrysothamnus nauseosus* Pall.) decreased from 1.1 to 0 percent. Of the four perennial grasses recorded in both 1960 and 1994, only Thurber's needlegrass increased in both absolute and relative cover. In terms of relative cover, perennial herbaceous species decreased from one-half of total cover to a little more than one-third, while shrub cover increased from one-third to two-fifths.

Western juniper cover more than doubled from 1961 (Table 2). Comparisons of aerial photographs taken in 1961, 1979, 1985, and 1994 show that the rate of increase was greatest between 1961 and 1979, but slowed (while still increasing) thereafter. We found numerous saplings throughout IRNA in June 1994. These young trees would have been too small to identify on the aerial photograph, but they suggest that future increases in

juniper cover are probable.

Two annual grasses were also recorded, cheatgrass and sixweeks fescue (*Vulpia octoflora* Rydb.), both of which decreased in absolute and relative abundance from 1960. The annual grass cover recorded in June 1994 may have been remnant from the previous year. The 1993 seasonal water-year (July 1, 1993 to June 30, 1994) was below average (7th driest on record), so little moisture was available for germination and growth of the annuals in the spring of 1994. Additionally, little snow fell during the previous winter, so the previous year's growth of annuals would not have matted down. By way of comparison, Driscoll may have experienced similar conditions in the summer of 1960 when precipitation during the 1959 seasonal water-year was also below average (the 27th driest on record). The reduction in the number of species recorded may also have been a function of drier conditions in 1994.

Table 1. Vegetation Cover, Composition, and Frequency by Classes and Species in IRNA Surveys of 1960 and 1994.

	1960			1994			Frequency ^c
	Cover ^a	Composition ^b	Standard Error	Cover	Composition	Standard Error	
Classes							
Total perennial herbs	14.2	50.0	—	14.0	35.5	1.32	245
Total shrubs	9.6	33.8	—	15.6	39.6	1.70	—
Total tree	4.6	16.2	—	9.8	24.9	0.46	—
Total perennial vegetation	28.4	100.0	—	39.4	100.0	—	—
Total annual vegetation	2.4	—	—	0.2	—	0.11	16
Total all vegetation	30.8	—	—	39.6	—	—	351
Species							
<i>Juniperus occidentalis</i> ^d	4.6	16.2	0.2	9.8 ^f	24.9	0.46	—
<i>Artemisia tridentata</i>	8.5	29.9	2.4	15.6 ^f	39.6	2.35	—
<i>Chrysothamnus nauseosus</i>	1.1	3.9	—	—	—	—	—
<i>Agropyron spicatum</i>	9.2	32.4	0.5	8.7 ^f	22.1	1.02	101
<i>Stipa thurberiana</i>	2.0	7.0	—	2.9	7.4	0.49	66
<i>Bromus tectorum</i> (A)	1.7	—	—	0.11	—	0.03	14
<i>Poa secunda</i>	1.3	4.6	0.3	1.7 ^f	4.3	0.35	31
<i>Lomatium triternatum</i>	0.6	2.1	—	0.2	0.5	0.06	11
<i>Vulpia octoflora</i> (A)	0.6	—	—	0.1	0.3	0.10	1
<i>Festuca idahoensis</i>	0.4	1.4	—	0.6	1.5	0.13	34
<i>Astragalus</i> sp.	0.3	1.0	—	—	—	0.00	0
<i>Agoseris</i> sp.	0.1	0.3	—	—	—	0.00	0
<i>Achillea millefolium</i>	0.1	0.3	—	0.0 ^e	—	0.01	1
<i>Collinsia parviflora</i> (A)	0.1	0.3	—	—	—	0.00	0
<i>Sitanion hystrix</i>	0.1	0.3	—	—	—	0.00	0
<i>Phlox douglasii</i>	0.1	0.3	—	—	—	0.00	0
<i>Cryptantha ambigua</i> (A)	—	—	—	0.0	—	0.01	1
<i>Eriogonum umbellatum</i>	—	—	—	0.0	—	0.01	1

Notes:

^aCover and composition values and standard errors from (Driscoll 1962).

^bComposition represents relative amounts of perennial species based on foliar cover.

^cFrequency represents the number of microplots where a species was present. Data for frequency collected on microplots only.

^dJuniper values determined by the authors' interpretation of 1961 and 1994 air photos.

^eValues of 0.0 indicate species present, but with cover < 0.1 percent.

^fA statistically significant difference based on independent Student t-test ($\alpha = 0.01$).

(A) = annual species.

Tree and Shrub Density, Shrub Heights

Both western juniper and big sagebrush density increased from 1960 (Tables 2 and 3). Tree density was 41 percent greater in 1994, and the density of big sagebrush increased significantly (by 115 percent). Rubber rabbitbrush density continued to be a minor component. The mean maximum height of big sagebrush was significantly greater—increasing by 50 percent. Basal area of perennial herbs also increased by 40 percent during the last 34 years. We have less confidence in this measurement, however, since it was difficult to distinguish with certainty the difference between live and dead biomass.

Confounding Influences

One of the most challenging questions for studies of vegetation change is how much of it is caused by humans and how much by natural environmental fluctuations? One of these human impacts is, of course, the increasing

atmospheric concentrations of CO₂ that accompanied the post-1800 industrial revolution. In order to assess the potential effects of CO₂ enrichment, it is necessary to study areas in non-laboratory settings where other human impacts and the impacts of fire, climate, and biotic influences have been minimal. Our study area satisfies these research conditions.

Table 2. Mean Number and Cover (percent) of *Juniperus occidentalis* on IRNA as Interpreted from Aerial Photographs^a.

Year	Number	Cover (percent)	Standard Error of Cover	Format	Approximate Scale	Mean Annual Precipitation (cm) ^b
1961	419	4.6	0.23	B&W	1:16,800	—
1979	526	8.7 ^c	0.23	B&W	1:8,950	27.8
1985	562	9.2 ^c	0.71	Blueprint	1:6,000	31.34
1994	590	9.8 ^c	0.46	Color	1:15,450	23.2

Notes: ^aAerial photographs were obtained from BLM (1961), Agricultural Stabilization and Conservation Service (1979), Oregon Department of Transportation (1985), and Thom Martin (1994).

^bThis value represents the average seasonal water-year precipitation for Prineville during the period between photographs (e.g., 27.8 cm = the mean annual precipitation between 1961 and 1979). Source: Karl et al. 1990.

^cCover is significantly different ($\alpha = 0.05$) from the 1961 value.

Climate

Since major changes in the regional macro-climate of IRNA could have influenced the structure and composition of the natural vegetation in the area, we examined various climate parameters for long-term trends and for significant differences between specific time periods.

Macroclimate Data. Climatic data for IRNA come from the South Central Climatic Division of Oregon (SCOR) and the Prineville 4NW weather station (Figure 2). Climatic division data (NCDC 1989), regionally derived and corrected for potential biases, are commonly used in examinations of long-term climatic conditions in the United States (e.g., Karl and Koscielny 1982; Diaz 1983; Soulé 1992). The Prineville station is the closest station to IRNA that is also included in the United States Historical Climatology Network (HCN). This station is approximately 43 kilometers southeast and 143 meters higher than IRNA. The HCN data for temperature and precipitation are regarded as the highest-quality data available for United States' stations. The data have been subjected to rigorous quality control checks and are corrected for biases in time-of-observation, instrument, and station movement (Karl et al. 1990). We obtained a complete record of mean monthly temperature and total precipitation for the period January 1895 to June 1994 for SCOR, and mean monthly temperature and precipitation data for Prineville for the period January 1900 to June 1994. Since HCN data were only available through April 1994, data for May and June of 1994 were obtained directly from the Office of the State Climatologist for Oregon (Taylor 1994). The Prineville record included 15 months of missing data (13 months of 1134 missing for temperature, 2 missing for precipitation). The majority (11) of the missing months for temperature occurred prior to 1927, and never did they run for more than two consecutive months. Missing data were replaced with HCN data from the nearby Bend station, located 50 kilometers south of IRNA at 1113 meters elevation (Figure 2). Missing precipitation data were transcribed directly from Bend, and temperature data were transcribed after correcting for elevation. In one instance (missing temperature data for December 1901), data were also missing for Bend, so the observation was replaced directly with data from the SCOR data set.

Table 3. Mean Values and Standard Errors of Perennial Basal Area on the IRNA Site.

	1960		1994	
	Value	Standard Error	Value	Standard Error
Basal area perennial herbs (percent)	6.6	0.7	9.23	0.89
Mean maximum height of <i>Artemisia tridentata</i> (cm)	59.4	3.35	89.39	3.27
Density count of <i>Artemisia tridentata</i>	26	3.2	56	0.46
Mean maximum height of <i>Chrysothamnus nauseosus</i>	61.9	—	71.20	—
Density count of <i>Chrysothamnus nauseosus</i>	4	—	1	—

Source: Driscoll 1962; authors' field surveys.

Macroclimate Methods. Because precipitation is largely concentrated in the low-sun sea-son in central Oregon (Sneva 1982), we calculated mean temperature and total precipitation based on July-to-June, or seasonal water-year, observations. We tested for significant differences in precipitation and temperature be-tween discrete time

periods using the Wilcoxon Rank Sum W Test and a null hypothesis of no significant difference in the climatic parameters between time periods, with a 0.05 level of significance. Since there were 34 years separating the two vegetation surveys, we tested for differences between the 34-year periods between the two surveys (1960-1993) and prior to Driscoll's survey (1926-1959). We also tested for differences between the 1960—1993 period and the remaining period of record (1900-1959 for Prineville data, 1895—1959 for SCOR data). Since Goldberg and Turner (1986) have shown that vegetation in arid regions can exhibit significant responses over brief periods (as short as 8-10 years), climatic variables were compared between the periods 1950-1959 and 1984-1993 using both the Wilcoxon test and a ranking scheme that shows how individual years in these two periods compare to observations over the period of record.

The climatic data were examined for linear trends over the two 34-year periods prior to vegetation sampling (1926-1959, 1960-1993) and over the combined 68-year period (1926—1993). We used temperature and precipitation as the dependent variables and seasonal water-year as the independent variable in a series of bivariate regressions. Numerous studies (e.g., Karl et al. 1986; Karl and Heim 1990; Plantico et al. 1990; Ids^o and Balling 1992; Yin 1993) have established the use of bivariate regression for trend analyses of climatic variables. We examined directional change in the climatic variables with trend slopes from the bivariate regression, and tested for significance in the trends using rank correlation (Yin 1993). For graphic presentation of long-term temperature and precipitation data, a weighted low-pass filter was used to smooth the time series (Panofsky and Brier 1968). The filter used is:

$$X_i = 0.06(i - 2) + 0.25(i - 1) + 0.38(i) + 0.25(i + 1) + 0.06(i + 2), \quad (1)$$

where X_i is the smoothed seasonal water-year temperature or precipitation and i = the current year in the time series.

Table 4. Annual Precipitation (cm) for Seasonal Water-Year (July to June) at Prineville, Oregon and the South-Central Climatic Division of Oregon.

Location and Years	N	Annual Mean	Standard Deviation	Median	High	Low
Prineville 1900–1993	94	24.9	6.5	24.1	43.0	11.6
South Central 1895–1993	99	30.5	6.1	30.1	45.5	18.0
Prineville 1926–1959	34	24.7	7.1	24.1	43.0	11.6
South Central 1926–1959	34	30.6	6.5	30.2	45.5	19.9
Prineville 1960–1993	34	26.4	7.4	25.6	39.7	12.4
South Central 1960–1993	34	30.8	6.9	29.5	42.7	18.0
Prineville 1950–1959	10	27.6	8.5	26.5	43.0	13.3
South Central 1950–1959	10	32.7	7.7	32.8	45.5	20.9
Prineville 1984–1993	10	23.4	6.6	23.4	35.7	12.9
South Central 1984–1993	10	28.4	5.7	27.9	41.9	22.6

Sources: NCDC 1989; Karl et al. 1990.

Macroclimate Results. The long-term precipitation records of Prineville and SCOR clearly illustrate the semiarid character of IRNA region (Table 4). In all cases the precipitation totals for the climatic division exceeded those of Prineville. Although the magnitude differs slightly, the Prineville and SCOR precipitation time series are strongly in-phase ($r = 0.83$ for a simple correlation of 1900-1993 data). Accordingly, we only present graphical results for Prineville. The 94-year pattern of seasonal water-year precipitation at Prineville shows that this region may experience considerable inter-year variability (Figure 5). The weighted low-pass filter shows that sustained directional changes in precipitation are generally on the order of 10 years or less.

Precipitation comparisons between the 34- and 10-year periods prior to the vegetation surveys yielded mixed results (Table 4). Although the 34-year period prior to Driscoll's survey was slightly drier and had less inter-year variability, comparisons of the 10-year periods show slightly wetter conditions with greater inter-year variability in the early period. Monotonic changes are not evident in either of the 34-year periods (Figure 5). This observation is supported by the linear-trend analysis (Table 5) that indicates weak and insignificant

positive trends in the early period (1926-1959) and even weaker trends in the later period (1960—1993). Precipitation trends over the 64-year period are also insignificant (Table 5).

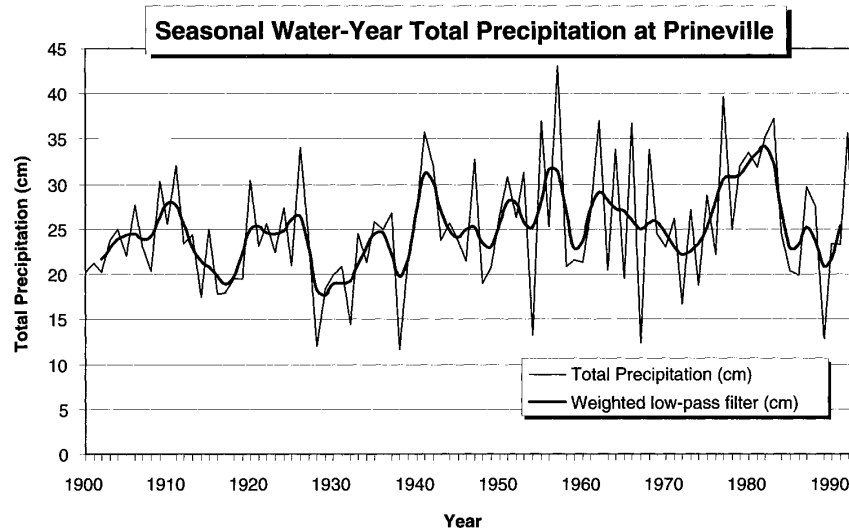


Figure 5. Season water-year (July–June) precipitation (cm) at Prineville, Oregon, 1900–1993. Source: Karl et al. 1990.

Mean seasonal water-year temperatures at Prineville are consistently higher than the regionally averaged measures for SCOR, with means for the former falling between 8 and 9° for all averaging periods (Table 6). As with precipitation, the temporal patterns are strongly in-phase ($r = 0.79$ for the 90-year period) between Prineville and SCOR. Although temperatures at Prineville do show a significant positive trend over the period 1926-1993 (Table 5), the trend was nearly flat for the early 34-year period and weakly positive for the late 34-year period, with most of the increase occurring between the late 1940s and late 1970s (Figure 6). A closer inspection of the 1926-1959 period and 1960-1993 period clearly shows the combination of slightly higher temperatures and lower inter-year variability in the later period (Figure 6).

Table 5. Climatic Parameters and Time: Bivariate Regression Slopes, Spearman Rank Correlation Coefficients, and Associated p-values.

Data Source	Variable	N	Time Period	Regression Slope	Spearman's r_s	p-value Spearman's r_s
Prineville	ppt.	68	1926–1993	0.061006	0.158	0.1991
South Central	ppt.	68	1926–1993	0.024952	0.048	0.7005
Prineville	ppt.	34	1926–1959	0.213655	0.270	0.1219
South Central	ppt.	34	1926–1959	0.189904	0.256	0.1440
Prineville	ppt.	34	1960–1993	-0.035762	-0.039	0.8262
South Central	ppt.	34	1960–1993	-0.033965	-0.065	0.7139
Prineville	temp	68	1926–1993	0.013435	0.394	0.0009 ^a
South Central	temp	68	1926–1993	0.004884	0.171	0.1631
Prineville	temp	34	1926–1959	-0.002269	-0.003	0.9877
South Central	temp	34	1926–1959	-0.009030	-0.094	0.5976
Prineville	temp	34	1960–1993	0.010958	0.171	0.3349
South Central	temp	34	1960–1993	0.015248	0.230	0.1913

Note: ^atrends significant at $\alpha = 0.05$.
Sources: NCDC 1989; Karl et al. 1990.

The 10-year period prior to the replicate survey was both hotter and received less precipitation than the 10-year period prior to Driscoll's survey. This is evident in both the descriptive statistics (Tables 4 and 6) and in rank comparisons for temperature (Table 7) and precipitation (Table 8). Both 10-year periods show a wide range in total precipitation, with years ranked among the top ten wettest and driest at Prineville and SCOR.

Variability (from above- to below-normal) in the thermal and moisture characteristics of both the short- (10-year) and longer-term (≥ 34 -year) periods is evident for all parameters examined. The lack of stability and persistence of the climatic parameters in the IRNA region support the finding of no significant differences in precipitation between any of the time period comparisons (Table 9). Temperature exhibits significant differences between the early and late 34- and 10-year periods at Prineville (the post-1960 periods being warmer), but all other comparisons indicate no significant differences (Table 9).

Table 6. Descriptive Temperature (°C) Statistics for Seasonal Water-Year (July to June) at Prineville, Oregon and the South-Central Climatic Division of Oregon.

Location and Years	N	Annual Mean	Standard Deviation	Median	High	Low
Prineville 1900–1993	94	8.4	0.7	8.4	10.5	6.9
South Central 1895–1993	99	7.9	0.7	7.8	10.2	5.7
Prineville 1926–1959	34	8.1	0.7	8.1	10.1	6.9
South Central 1926–1959	34	7.8	0.7	7.9	10.2	6.4
Prineville 1960–1993	34	8.6	0.6	8.6	10.5	7.4
South Central 1960–1993	34	8.0	0.6	8.0	10.1	7.1
Prineville 1950–1959	10	8.2	0.6	8.1	8.8	7.2
South Central 1950–1959	10	7.8	0.7	7.9	8.8	6.6
Prineville 1984–1993	10	8.8	0.8	8.7	10.5	7.6
South Central 1984–1993	10	8.3	0.8	8.3	10.1	7.3

Sources: NCDC 1989; Karl et al. 1990.

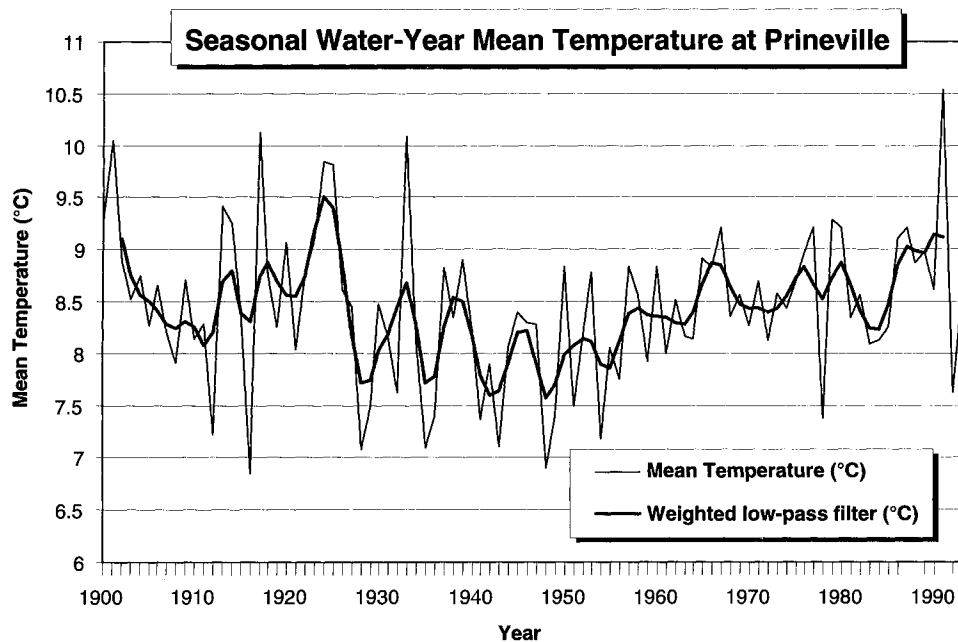


Figure 6. Seasonal water-year (July–June) temperature (°C) at Prineville, Oregon, 1900–1993. Source: Karl et al. 1990.

We also examined the 24-month periods prior to Driscoll's vegetation survey (July 1958 to June 1960 or the early period) and our replicate survey (July 1992 to June 1994 or the late period) because of the possibility of vegetation change caused by short-term variability (Mueggler 1992). The Prineville precipitation record shows that total precipitation over the early 24-month period was 42.4 cm as compared to 52.1 cm for the late period. A Wilcoxon test indicated no significant differences in precipitation between the two 24-month periods ($p = 0.4212$; Figure 7). Monthly mean temperatures for the two periods were generally in-phase (Figure 8), with a 24-month mean of 8.2°C for the early period and 8.1°C for the late period. A Wilcoxon test showed no significant difference in temperature between the periods ($p = 0.9343$).

Relating Macroclimatic Change to Vegetation. Clearly, the climate is not stable. Regime changes from wetter-to-drier than normal and hotter-to-cooler than normal can occur over short time periods in the IRNA region and have occurred within the time periods prior to the initial and replicate vegetation surveys. Note, however, that the climatic parameter most critical for vegetation growth (precipitation) is not significantly different for the periods prior to both vegetation surveys.

Microclimate. When Driscoll conducted his vegetation survey in 1960, the IRNA was bounded on the west by

the Deschutes River and on the east by the Crooked River (Figure 2). The elevation of the two river beds at the time was approximately 550 meters. Subsequent to Driscoll's benchmark study, the Crooked and Deschutes Rivers were dammed, and Lake Billy Chinook was created in 1963. The lake surrounds the IRNA on 3 sides (Figure 2), and has a normal pool elevation of 593 meters (USGS 1993).

Table 7. 94-Year and 99-Year Rankings of Seasonal Water-Year (July to June) Temperatures (°C) at Prineville, Oregon and the South Central Climatic Division of Oregon, Respectively, for the 10-Year Period Preceding Driscoll's Vegetation Survey and the 10-Year Period Preceding the 1994 Replicate Survey.

Prineville, Oregon					
1950 to 1959			1984 to 1993		
Rank ^a	Year	Temp (°C)	Rank	Year	Temp (°C)
6 ^b	1954	7.2	15	1992	7.6
13	1951	7.5	26	1984	8.1
16	1956	7.8	36	1985	8.3
19	1959	7.9	55	1993	8.6
22	1955	8.1	57	1990	8.6
32	1952	8.2	72	1988	8.9
52	1958	8.6	77	1989	9.0
66	1953	8.8	80	1986	9.1
70	1950	8.8	84	1987	9.2
71	1957	8.8	94 ^c	1991	10.5
$\Sigma_{\text{rank}} = 367$			$\Sigma_{\text{rank}} = 596$		
$\bar{X}_{\text{rank}} = 36.7$			$\bar{X}_{\text{rank}} = 59.6$		

South Central Climatic Division, Oregon					
1950 to 1959			1984 to 1993		
Rank ^a	Year	Temp (°C)	Rank	Year	Temp (°C)
4 ^b	1954	6.6	16	1984	7.3
12	1951	7.2	24	1992	7.4
25	1955	7.4	54	1985	7.9
27	1956	7.5	68	1993	8.1
39	1959	7.7	75	1990	8.2
55	1952	8.0	79	1988	8.3
63	1957	8.1	82	1989	8.4
80	1953	8.4	90 ^c	1987	8.6
81	1950	8.4	93 ^c	1986	8.7
94 ^c	1958	8.8	98 ^c	1991	10.1
$\Sigma_{\text{rank}} = 480$			$\Sigma_{\text{rank}} = 679$		
$\bar{X}_{\text{rank}} = 48.0$			$\bar{X}_{\text{rank}} = 67.9$		

Notes: ^arank is based on 94 years of data (1900–1993) for Prineville and 99 years of data (1895–1993) for the South Central Climatic Division.
^bone of the ten coldest years.
^cone of the ten hottest years.
Sources: NCDC 1989; Karl et al. 1990.

Table 8. 94-Year and 99-Year Rankings of Seasonal Water-Year (July to June) Precipitation (cm) at Prineville, Oregon and the South Central Climatic Division of Oregon, Respectively, for the 10-Year Period Preceding Driscoll's Vegetation Survey and the 10-Year Period Preceding the 1994 Replicate Survey.

Prineville, Oregon					
1950 to 1959			1984 to 1993		
Rank ^a	Year	PPT (cm)	Rank	Year	PPT (cm)
5 ^b	1954	13.3	4 ^b	1989	12.9
27	1958	20.9	7 ^b	1993	16.4
33	1959	21.6	19	1986	19.9
56	1956	25.4	23	1985	20.4
62	1952	26.3	41	1991	23.3
63	1950	26.7	44	1990	23.5
75	1951	30.8	51	1984	24.5
76	1953	31.3	70	1988	27.7
91 ^c	1955	37.0	72	1987	29.8
94 ^c	1957	43.0	87 ^c	1992	35.7
$\Sigma_{\text{rank}} = 582$			$\Sigma_{\text{rank}} = 418$		
$\bar{X}_{\text{rank}} = 58.2$			$\bar{X}_{\text{rank}} = 41.8$		

South Central Climatic Division, Oregon					
1950 to 1959			1984 to 1993		
Rank ^a	Year	PPT (cm)	Rank	Year	PPT (cm)
6 ^b	1954	20.9	7 ^b	1993	22.6
18	1958	24.2	9 ^b	1991	22.9
27	1959	26.8	17	1989	23.8
60	1950	31.9	28	1986	26.9
65	1953	32.6	33	1990	27.3
67	1951	32.9	39	1984	28.4
69	1952	33.4	41	1987	28.6
77	1956	34.9	49	1988	30.0
98 ^c	1957	43.5	58	1985	31.8
99 ^c	1955	45.5	96 ^c	1992	41.9
$\Sigma_{\text{rank}} = 586$			$\Sigma_{\text{rank}} = 377$		
$\bar{X}_{\text{rank}} = 58.6$			$\bar{X}_{\text{rank}} = 37.7$		

Notes: ^arank is based on 94 years of data (1900–1993) for Prineville and 99 years of data (1895–1993) for the South Central Climatic Division.
^bone of the ten driest years.
^cone of the ten wettest years.
Sources: NCDC 1989; Karl et al. 1990.

It is doubtful the creation of Lake Billy Chinook in 1963 had any significant impacts on vegetation growth (e.g., increased precipitation) in the IRNA. Micro-scale oasis effects can be detected over irrigated fields (Fritschen and Nixon 1967; Oke 1987), but the effects (reduced temperature, increased vapor pressure) typically decay rapidly within the first 1.5 m above the surface (Fritschen and Nixon 1967). Further, most microclimatic effects in arid environments are contained within and near (30 m downwind) the boundaries of irrigated areas because convection tends to dominate over advection (Fritschen and Nixon 1967). Because of the vertical distance (averaging over 130 m) from the IRNA plateau to the lake surfaces, the small surface area of the lakes (compared to large-scale irrigation projects of 100,000+ ha), and the well-ventilated nature of the plateau, it is unlikely that oasis effects (whereby relative humidity and vapor pressures would be increased and temperatures decreased over the lake surface [Oke 1987]) would extend to the plateau. If evaporation from the lake surface

had any effects on the microclimate of the IRNA plateau, these effects should be most evident at the plateau edge and least evident in the plateau center. We conducted a microclimatic study on the IRNA plateau to test for edge-to-center differences in surface temperature, temperature at 1 m elevation, soil temperature, and relative humidity at 1 m elevation. Results of the microclimatic analysis showed no significant differences in any parameter and that stable conditions prevailed across the plateau.

Table 9. Precipitation and Temperature Differences by Periods, Wilcoxon Rank Sum *W* Test Results.

Data Source	Variable	Time Periods Compared	Test p-value	Result
Prineville	ppt.	1900–1959 / 1960–1993	0.1308	accept H_0
South Central	ppt.	1895–1959 / 1960–1993	0.9237	accept H_0
Prineville	ppt.	1926–1959 / 1960–1993	0.3481	accept H_0
South Central	ppt.	1926–1959 / 1960–1993	0.9706	accept H_0
Prineville	ppt.	1950–1959 / 1984–1993	0.1859	accept H_0
South Central	ppt.	1950–1959 / 1984–1993	0.1212	accept H_0
Prineville	temp	1900–1959 / 1960–1993	0.0553	accept H_0
South Central	temp	1895–1959 / 1960–1993	0.0996	accept H_0
Prineville	temp	1926–1959 / 1960–1993	0.0005	reject H_0
South Central	temp	1926–1959 / 1960–1993	0.1999	accept H_0
Prineville	temp	1950–1959 / 1984–1993	0.0451	reject H_0
South Central	temp	1950–1959 / 1984–1993	0.2123	accept H_0

Note: All tests are conducted at $\alpha = 0.05$ with H_0 : the distribution of measurements for the two time periods are equal. Sources: NCDC 1989; Karl et al. 1990.

Fire

Fire likewise may confound our comparison of the 1960 and 1994 vegetation surveys. We were particularly concerned about this issue, since Driscoll (1964) believed, based on the number of charred stumps and logs present, that fires had influenced the density of western junipers on IRNA. Driscoll also reported that "in a few small areas" fires had eliminated both the tree and shrub associations, and in these areas an herbaceous stratum had become dominant (but not in his macroplots). Conversely, our 1994 survey yielded no evidence of recent fires, though we did find areas where shrub and tree density were low and grass cover was dominant—possibly the same areas mentioned by Driscoll in 1960.

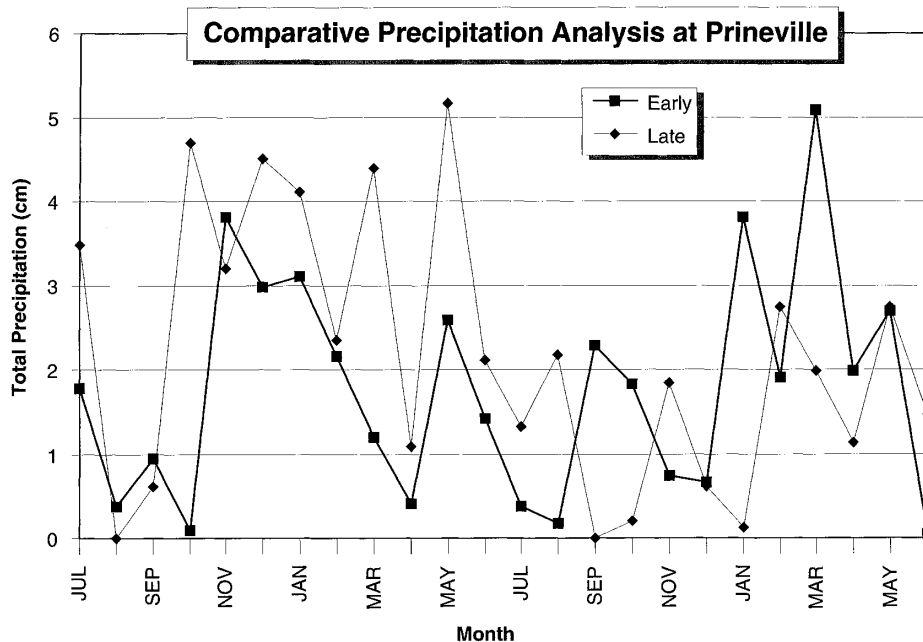


Figure 7. Comparison of monthly precipitation (cm) at Prineville, Oregon in the 24-month period prior to Driscoll's vegetation survey (July 1958 to June 1960—early) and the 24-month period prior to the replicate survey (July 1992 to June 1994—late). Source: Karl et al. 1990.

We then examined the fire history of IRNA since 1960. Because the land ownership of IRNA is split between the United States Forest Service (USFS), the Bureau of Land Management (BLM), and Oregon State Parks (OSP), we interviewed personnel from each agency, including the Fire Management Officer for the Prineville BLM, the District Ranger for the Ochoco National Forest, a Naturalist for Cove Palisades State Park (CPSP),

and a former CPSP ranger. We also examined a document file for IRNA at the Prineville BLM. By all accounts, only two fires on IRNA have been reported since Driscoll's study. Both occurred on the same day in late August 1987 and both were caused by lightning strikes. The CPSP ranger on duty at the time told us that he and one other CPSP personnel had climbed the trail to IRNA to extinguish the fires (Smith 1994). One lightning bolt had struck a juniper on the south-east end of IRNA, but the fire was out (smoldering) by the time they arrived. The second lightning strike had created a small fire, which burned approximately one-thirtieth of a hectare (9 m × 36 m) near the northwest rim before it was extinguished with hand tools. The CPSP ranger told us that it was unlikely that the fires would have expanded, because wind conditions at the time were characterized as a "light breeze" and the fuel continuity necessary for the fire to carry was insufficient (patchy).

We were also interested in learning how the lack of fire on IRNA was related to vegetation associations in similar areas where fire records have been kept. To acquire this knowledge, we analyzed fire statistics from 1970-1993 for the 42,400-hectare Crooked River National Grassland (CRNG) whose boundaries encompass IRNA. Data for this region afford the best opportunity for comparison since the majority of the CRNG is characterized by topography and vegetation similar to IRNA.

The frequency of lightning-caused fires indicates that fire has not been a major disruptive force on the CRNG during the past quarter-century. Between 1970 and 1993, 52 lightning-caused fires occurred on the CRNG. The annual number of fires ranged from 0 (seven different years) to 11 (once). Two factors appear to be responsible for the infrequency of fires: 1) a low frequency (between 6-20 days/year) of thunderstorms in central Oregon (Keen 1987); and 2) insufficient fuel continuity to carry the fire (Knapp 1995). Thus, the two fires on the 78 ha IRNA since 1960 are not inconsistent with the low incidence of fire in the larger region.

Wildfires on relict intermountain environments are infrequent. Whisenant (1990) reported that mean fire-return intervals in minimally disturbed sagebrush-steppe communities likely ranged from 60 to 110 years, with the longer intervals of a century assigned to the driest environments with big sagebrush present (Wright and Bailey 1982). Additionally, many researchers (e.g., West 1983; Young et al. 1987; Whisenant 1990) in areas where fires are frequent (< 5 years) have identified a continuous fuelbed of exotic, annual grasses as the primary cause. These grasses likely expanded into sagebrush-steppe environments because of overgrazing, but their maintenance (or expansion) typically is perpetuated by frequent fires that substantially reduce the cover and density of competing shrubs and perennial grasses (West 1983). There is no evidence to suggest that this annual grass/wildfire cycle exists on IRNA, that is, it appears not to be a significant confounding influence.

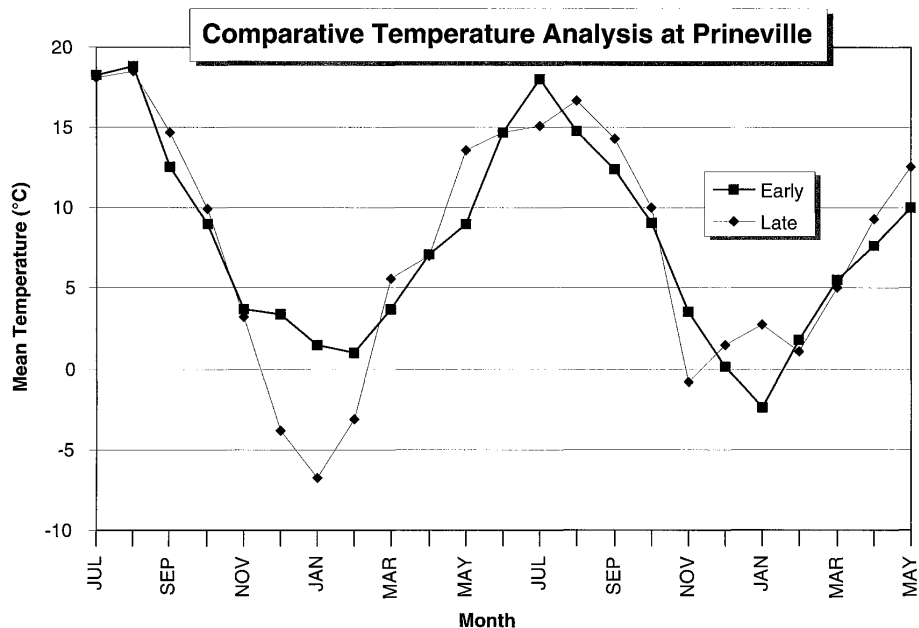


Figure 8. Comparison of mean monthly temperature (°C) at Prineville, Oregon in the 24-month period prior to Driscoll's vegetation survey (July 1958 to June 1960—early) and the 24-month period prior to the replicate survey (July 1992 to June 1994—late). Source: Karl et al. 1990.

Biotic Influences

Two biotic influences known to cause shrub die-off in the western states, plant disease and herbivory, are also unlikely to have had significant influences on IRNA vegetation. Plant disease in western shrubs is thought to be caused by increased precipitation that in turn increases soil salinity and decreases soil oxygen (Weber et al. 1990)—changes that predispose shrubs to attacks by pathogenic root rot organisms. This impact seems to be most evident for species associated with poorly drained soils, but this association is not the case on IRNA. The fractured basaltic origin and upland location of IRNA make for well-drained soils. Indeed as Lunt et al. (1973) have shown, the high soil oxygen requirements of big sagebrush generally excludes it from poorly drained soils.

Herbivory by grazing animals also is unlikely to have affected the results. The grazing pressures of mule deer on IRNA appear to be minimal because of the lack of a water source on the plateau and the distance (horizontal and vertical) separating the plateau from surrounding water sources (Figure 4). Finally, while grazing by small mammals or insects (e.g., grasshoppers) during periodic population fluctuations may cause vegetation change for short (1 to 2 years) periods (Mueggler 1992), these population fluctuations are typically triggered by favorable climatic conditions. And as our climatic analyses show, differences in precipitation or temperature in the two years prior to each study period are not statistically significant. Moreover, BLM records compiled during the last 20 years also report no outbreaks of intense herbivory on IRNA.

Discussion

Johnson et al. (1993) have argued that the relationship between atmospheric carbon di-oxide and competition is manifested through differential growth rates of individual species that modify the ability of species to acquire and use other necessary resources. Varying growth rates cause differences in light interception rates that confer a competitive advantage on those species that shade out other species, or that have greater leaf area to absorb more light (Bazzaz and Fajer 1992). The differential effects of increased carbon supply on species also alters competitive interactions through changes in habitat requirements, rates of acquisition of scarce growth resources, rates of growth and phenological development timing, and changes in the required amounts of specific growth resources necessary for ecological success (Johnson et al. 1993).

Woody Species

Our results are in general agreement with proposed CO₂ theories. Cover increased for big sagebrush and western juniper, and slightly decreased for perennial grass cover. In terms of relative cover, most woody species experienced major increases while the dominant herbaceous species experienced reductions.

Big Sagebrush. The largest absolute increase was for big sagebrush, one of the few species native to IRNA that has been examined for response to various atmospheric CO₂ levels. Johnson and Lincoln's (1990) study of big sagebrush recorded growth responses at three levels of atmospheric carbon dioxide—270, 350, and 650 ppm—for plants of three to nine weeks growth. Elevating carbon dioxide from 270 to 350 ppm increased leaf biomass, leaf area, specific leaf weight and plant biomass by 38, 6.5, 35, and 59 percent, respectively. Further increases in carbon dioxide levels from 350 ppm to 650 ppm resulted in additional increases in leaf biomass (46 percent), leaf area (67 percent), and plant biomass (9.6 percent). This evidence suggests a continuing stimulatory effect of atmospheric CO₂ enrichment beyond current CO₂ levels.

At the IRNA site, sagebrush density more than doubled during the last 34 years. These results are in general agreement with other studies that have looked at long-term vegetation changes in arid and semiarid regions under a variety of land-uses. On the sagebrush-steppe of the Upper Snake River Plains of Idaho, for example, sagebrush density increased by 60 percent between 1948 and 1966 (Harniss and Murray 1973). This area had been grazed by sheep each spring and fall, but the authors concluded that "good grazing management [would] not prevent sagebrush reinvasion" (p. 325). Studies in sagebrush-steppe environments in the Great Basin and southwestern Montana also report large increases in sagebrush density over 50-to-100 year intervals (Rogers 1982; Knapp 1991). These changes are attributed to altered fire intervals and changing land-use practices. Similarly, Goldberg and Turner (1986) examined vegetation changes over a 72-year period (1906—1978) on fenced permanent plots in the Sonoran Desert. In a majority of these plots, shrub density consistently increased,

which may have been a response to cessation of cattle, sheep, and horse grazing from 1858 to 1906.

Increases in sagebrush cover were also impressive on IRNA between 1960 and 1994. The near doubling in this case is consistent with other long-term studies. For example, Anderson and Nolte (1981) found that sagebrush cover increased by 154 percent between 1950 and 1975 on permanent vegetation transects protected from grazing for 25 years in south-eastern Idaho.

Similarly, mean sagebrush height at IRNA increased over 30 cm since 1960. Under favorable conditions, big sagebrush can exceed 4.5 meters (Mozingo 1987), so this increase is not surprising given the more favorable conditions (i.e., higher CO₂) during the last 34 years.

Big sagebrush typically grows in steppe environments with annual precipitation totals between 18 to 40 cm (Mozingo 1987). Idso (1989) has argued that increases in WUE should result in proportional decreases in the amount of precipitation required for survival. Since precipitation totals for IRNA are near the lower range for big sagebrush, increases in WUE would seem to provide the impetus for increases in density, cover, and height. Additionally, big sagebrush has evolved the ability to cope with drought by dropping some of its leaves and by concentrating salts in the cell sap (Mozingo 1987). These adaptations to drought are of particular importance, since Rozema (1993) and Idso and Idso (1994) have reported that atmospheric CO₂ partially alleviates the drought's deleterious effects for a variety of plants grown under drought stress.

Western Juniper. Western juniper also experienced large increases in density and cover during the past 34 years. This slow-growing and long-lived tree (800-1000+ years) is principally found in central Oregon with disjunct populations in bordering states (Preston 1968; Caraher 1978). It does well on exposed, rocky sites, is windfirm (Preston 1967), and requires a minimal precipitation of 25 cm/year—approximately the annual total on IRNA.

Evidence of widespread western juniper establishment is supported by written and photographic records as well as dendrochronological analyses. Burkhardt and Tisdale (1969; 1976) examined four western juniper sites in southwestern Idaho and determined that the cessation of natural fires, particularly since 1910, was the principal cause of juniper establishment. Additionally, they believed that fire frequencies decreased because of active fire control and prevention, reduction of phytomass by grazing, construction of fire breaks such as roads, and a warmer and drier climate during the past century. Similarly, Caraher (1978), Eddleman (1987), and Miller and Rose (1995) reported large increases of western juniper (on sites exposed to a variety of land-use activities) into big sagebrush communities in Oregon during the last 100 years. Possible causes for the establishment were seed dispersal by birds, fire cessation, increases in sagebrush, and the influences of grazing (Caraher 1978; Eddleman 1987; Miller and Rose 1995). In addition, Miller and Wigand (1994) have suggested that increasing atmospheric CO₂ conditions may also play a role.

Our results on western juniper, like those presented by Eddleman (1987) and Miller and Rose (1995), suggest that establishment is occurring across a variety of land-uses. Eddleman (1987) found that the oldest trees on his study site were established in 1880 and that juniper density continually increased through the end of his study period in 1980. Eddleman's results are in agreement with those of Miller and Rose (1995). They cored 1200 western juniper on Steens Mountain in southeastern Oregon to determine establishment dates and found substantial juniper expansion began in the 1880s, and continued through the 1950s. From the 1960s onward, however, juniper establishment "then began to progress at a geometric rate" (Miller and Rose 1995:37), and occurred in the absence of favorable climatic conditions. Similarly, we found that juniper density and cover increased at each interval measured between 1961 and 1994.

Western juniper establishment on IRNA seems to have occurred without the operation of the traditional mechanisms used to explain the increases elsewhere. If western juniper cover and density have increased because of decreased fire-return intervals, then these are naturally occurring phenomena and are not promoted by changing land-use activities. Domestic grazing, viewed as an indirect catalyst because it decreases the amount of fine fuel necessary to carry a fire, has been absent (and likely never was a factor) on IRNA for

approximately 70 years. Climatic variability has been statistically insignificant since 1960 with the exception of a slight increase in temperature. Miller and Wigand (1994:446) have shown that previous episodes of western juniper expansion during the Holocene (beginning "between 4000 and 7000 years ago") in eastern Oregon occurred under wetter conditions. Conversely, the most recent (post-1880s) episode of juniper expansion has occurred under more arid conditions that are considered to be unfavorable for juniper establishment (Miller and Wigand 1994).

What, then, has caused the increase in juniper density and cover? We believe at least two causes are responsible for the IRNA increase. First, elevated CO₂ during the past 34 years likely has increased WUE for the western juniper, thereby making a climatically marginal juniper site (lower end of precipitation requirements) more favorable. Although we lack studies relating western juniper expansion to elevated atmospheric CO₂ and associated increases in WUE, Hollinger (1987) has shown that Douglas fir (*Pseudotsuga menziesii*) and Monterey pine (*Pinus radiata*), both western conifers, increased the levels of WUE at CO₂ concentrations of 640 ppm. Additionally, La Marche et al. (1984), Graybill (1987), and Graybill and Idso (1993) have reported probable and substantial CO₂ growth-enhancement beginning in the latter half of the nineteenth century for subalpine conifers (particularly the "strip-bark" tree form) growing under natural conditions on semiarid sites in the Sierra Nevada, Southern Rockies, and Great Basin. Graybill (1987) and Graybill and Idso (1993) have noted that growth enhancement may have been a function of increased WUE.

A second cause of juniper establishment may be related to the increase in big sagebrush cover and density. Increases in the latter have created more favorable sites for juniper germination and establishment. Burkhardt and Tisdale (1976) and Eddleman (1987) have suggested that western juniper establishment typically begins beneath the canopy of big sage-brush plants, probably because these locations are preferred nesting sites for local bird species that use juniper berries as a food source. It has been further suggested that big sagebrush acts as a nurse plant for juniper seedlings where the seedlings benefit from the microclimatic conditions (reduced temperature variability, reduced transpiration rates) and elevated nutrient status near the shrub base. We noted many western juniper saplings growing within the canopy of big sagebrush.

Herbaceous Species

Our vegetation survey reported little change in total perennial herbaceous cover and a decrease in annual cover during the past 34 years. The dominance of perennial herbaceous species, however, decreased from 50 percent of the relative cover to 35.5 percent. Studies that have monitored long-term change on sagebrush-steppe grasslands have reported a variety of results. Anderson and Nolte (1981) found that in a southeastern Idaho exclosure, perennial grass cover increased from 0.3 percent to 5.8 percent after 25 years without grazing. In another study in southeastern Idaho, Harniss and Murray (1973) found that herbaceous species yield (including bluebunch wheatgrass) decreased between the years 1936-1966 and was likely a function of vigorous sagebrush establishment following a burn.

Our results, similar to Harniss and Murray (1973), indicate a decrease in perennial herbaceous cover. It appears that grass cover has been able to coexist with woody species with only a slight decrease in absolute cover. This may be because of various responses of individual species to elevated CO₂, competition dynamics for light and nutrients, and/or the fact that the herbaceous vegetation cover is susceptible to yearly variations in herbivory and precipitation (Mueggler 1992).

Few laboratory studies have examined the effects of CO₂ enrichment on herbaceous species common to central Oregon. Smith et al. (1987) have done so, however, for four Great Basin grasses including cheatgrass and western wheatgrass (*Agropyron smithii* Rydb.). When these grasses were grown in atmospheric CO₂ concentrations of approximately the ambient atmosphere (340 $\mu\text{l l}^{-1}$) and double the ambient atmosphere (680 $\mu\text{l l}^{-1}$), cheatgrass had the most consistent response. CO₂ enrichment significantly increased above-ground dry weight, the number of basal stems, and the leaf area of cheatgrass 120 days after seedling emergence relative to ambient conditions. For western wheatgrass, significant increases were reported for the number of basal stems, above ground dry weight, and specific leaf weight, but not leaf area.

The decrease in IRNA's cheatgrass cover was the only measurement that we felt was inconsistent with the theory of atmospheric CO₂ enrichment. Based on laboratory results and the widespread distribution of cheatgrass (Mack 1981; Young et al. 1987), we anticipated greater cover at IRNA. This inconsistency may be because annuals such as cheatgrass are opportunists that take advantage of favorable events as they occur; hence, cover variability would be linked principally to favorable climatic conditions. Cheatgrass germinates in the fall after the first rain, its roots grow throughout most of the winter (temperatures must be above 0°C), and above-ground biomass is dependent on spring soil moisture (Harris 1967; West 1983). While precipitation totals were similar in the two years preceding the 1960 and 1994 studies, a closer look reveals that March precipitation in 1960 was above normal, that is, sufficient to encourage abundant cheatgrass growth in the spring of 1960.

Conclusions

We realize that the cause of vegetation change in any plant community is often a function of numerous factors either working individually or in concert, and that it is difficult to separate these mechanisms. We also realize that plant communities change continuously. Our purpose, however, is to determine if the increases in woody species cover and density are explicable by traditional mechanisms; or, if not, are these increases consistent with what has been predicted to occur as a result of atmospheric CO₂ enrichment? For vegetation change on IRNA, we believe that the latter phenomenon has been operative. We found no statistically significant different periods of precipitation for the 2-, 10-, and 34-year periods before each study date. Nor did fire appear to be a significant component of vegetation dynamics on IRNA. IRNA's fire history is meager (only one incident between 1960 and 1994), and the two fires that did occur did not affect our study area (macroplots). Furthermore, grazing has not occurred for approximately 70 years, insect or disease impacts were not found, and human activity on IRNA was minimal. In sum, neither Driscoll's survey nor ours was subject to unusual perturbations that would have affected our comparison of vegetation change.

IRNA's vegetation changes are generally consistent with outcomes predicted by both laboratory and controlled field experiments employing elevated levels of atmospheric CO₂; and they are similar to much of what has been reported in other long-term studies in natural sites exposed to a variety of land-use practices (i.e., fire, grazing) in sagebrush-steppe environments. Our results suggest that atmospheric CO₂ enrichment is a likely contributory cause of vegetation change on IRNA, and more specifically, to increases in woody species that now represent nearly two-thirds of the total vegetation cover. As IRNA's western juniper and big sagebrush density increased (by 41 percent and 115 percent, respectively), its perennial herbaceous cover was nearly unchanged and annual grass cover decreased.

IRNA's protected status and the permanency of the plots invite further studies of the affects of CO₂ enrichment on vegetation. First, controlled laboratory experiments that expose the native dominants to elevated CO₂ levels would provide insight into the relative responses of the species. Second, replicate quinquennial surveys would eliminate the caveats associated with the two "snapshot" samples used here. Third, comparative studies could provide benchmarks for similar repeat surveys in other protected sagebrush-steppe areas. Fourth, dendrochronological analyses of IRNA's western juniper would determine establishment dates, and would help elucidate the rate of juniper expansion following the industrial revolution. Finally, as Neilson (1993) has argued, ecotones may be particularly good sites to observe vegetation changes in response to atmospheric changes. Monitoring of ecotones (e.g. sagebrush-steppe/ponderosa pine) common to central Oregon would also provide in-sight.

This study seeks to understand long-term vegetation change when familiar explanations fail. While the relationship between rising atmospheric CO₂ concentrations and increases in woody species may seem fortuitous, we believe that this relationship is more than coincidental. The implications of these results for natural ecosystems are broad. Regionally, continual shifts toward increased woody-species cover and density in sagebrush-steppe and juniper woodlands of the American West would alter fire regimes, range productivity, and watershed dynamics. Globally, Idso and Kimball (1993) have argued that enhanced tree (woody) growth increases forest biomass, thus resulting in more niche availability that favors higher biodiversity. Further, they

state (p. 551) that "enhanced tree growth would greatly augment the biospheric removal of carbon dioxide from the atmosphere," thus altering the rate of increases in CO₂ and complicating the associated consequences of these increases (e.g., possible global warming). Clearly, given the ubiquitous nature of atmospheric CO₂ enrichment and the probable effects to vegetation, additional studies from other relict sites are necessary to lend credence to the global-scale dynamics of CO₂ - enhanced vegetation change suggested herein.

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