

CHANGING PERCEPTIONS OF PRE-EUROPEAN GRASSLANDS IN CALIFORNIA

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ABSTRACT

The grasslands of California are dominated by non-native annual grasses primarily of Mediterranean origin. Because replacement of native species occurred before extensive botanical study, the original extent and composition of native vegetation is unknown. In 1920, the influential ecologist F. E. Clements concluded that widely scattered patches of perennial bunchgrass were 'relicts' of a once vast perennial grassland. He proposed that the pre-European vegetation of the Central Valley, the valleys of southern California, and many areas of the Coast Ranges were originally dominated by the perennial grass *Nassella pulchra*. Although this hypothesis has become widely accepted, analysis of the data indicates that, especially for central and southern California, this hypothesis is probably incorrect. Clements made a number of mistakes including misidentification of important taxa, over-reliance on his putative 'relicts', misunderstanding of the role of fire in grassland communities, and taking other people's work out of context. Alternative hypotheses have existed for almost as long as Clements' original hypothesis, but these have been generally ignored both by Clements and by many subsequent researchers in the field. There is a growing body of evidence to suggest that many of the areas dominated today by non-native annual grasses may formerly have been dominated by different vegetation types such as oak woodland, chaparral, or coastal scrub.

KEY WORDS: *Nassella pulchra*; *Stipa pulchra*; California grasslands; bunchgrasses; F. E. Clements

Today, large areas of California are dominated by non-native annual grasses primarily of Mediterranean origin. The contemporary temperate grasslands of western North America represent dramatic examples of large scale species replacement due to plant invasions (Mack 1989). In particular, much of central and southern California has been invaded to such an extent and so rapidly by non-native plant species that the original extent and composition of native vegetation will probably never be known with certainty (Keeley 1989; Heady et al. 1992). The native vegetation was destroyed (probably due primarily to overgrazing from domestic livestock) before any significant botanical collections were made (Burcham 1957; Baker 1978). Despite this, the idea that areas that are now dominated by non-native annual grasses were originally dominated by perennial bunchgrasses (primarily *Nassella pulchra*; see Table 1) has been so widely adopted as to be practically axiomatic (e.g., Burcham 1957; Barry 1972; Heady 1977; Fradkin 1995). Grasslands of northwestern

TABLE 1. NOMENCLATURAL CHANGES FOR IMPORTANT SPECIES OF GRASSES IN THE CALIFORNIA GRASSLANDS MENTIONED IN THE TEXT

Name used in the California literature	Period used	Name used in The Jepson Manual 1993
<i>Stipa setigera</i> Presl	1865–1933	<i>Nassella pulchra</i> sensu lato (sensu lato indicates <i>N. pulchra</i> + <i>N. cernua</i>)
<i>Stipa eminens</i> Cav.	1865–1939	<i>Nassella lepida</i> (A. Hitchc.) Barkworth
<i>Stipa pulchra</i> Hitchc.	1915–1941	<i>Nassella pulchra</i> (A. Hitchc.) Barkworth sensu lato
<i>Stipa pulchra</i> Hitchc.	1941–1993	<i>Nassella pulchra</i> (A. Hitchc.) Barkworth sensu strict.
<i>Stipa cernua</i> Stebb. & Love	1941–1993	<i>Nassella cernua</i> (Stebb. & Love) Barkworth
<i>Stipa lepida</i> Hitchc.	1915–1993	<i>Nassella lepida</i> (A. Hitchc.) Barkworth
<i>Stipa lemmoni</i> (Vasey) Scribn.	1901–1993	<i>Achnatherum lemmonii</i> (Vasey) Barkworth
<i>Elymus triticoides</i> Buckl.	1862–1993	<i>Leymus triticoides</i> (Buckley) Pilger
<i>Festuca megalura</i> Nutt.	1848–1974	<i>Vulpia myuros</i> (L.) C. Gmelin

California form a different community type (Munz and Keck 1950) and are not the subject of this review.

The idea that the pre-European vegetation of the Central Valley, the central and southern Coast Ranges, and valleys of southern California was perennial grassland was first proposed by the influential ecologist F. E. Clements (1920). What was the evidence on which this hypothesis was based? Why has this particular hypothesis enjoyed such acceptance when there have also been a number of alternative hypotheses proposed? In this review, the history of Clements' ideas and how they implicitly and explicitly continue to affect people's views, scientific research, and land management practices are considered. In addition, current thinking on floristic composition and extent of grasslands in California is summarized.

Human understanding improves by building on the work of the past. In order to keep progressing, however, it is sometimes necessary to look back to reevaluate the firmness of the foundation on which we stand. The intellectual history of grasslands in California forms a cautionary tale where force of personality, uncritical acceptance of hypotheses, and weight of scientific authority have sometimes overshadowed data and squelched open debate so important for the progress of science.

A BRIEF TAXONOMIC HISTORY OF *NASSELLA PULCHRA*

To understand the history of thought concerning grasslands in California, it is necessary to review the nomenclatural changes for

the most important native perennial grasses (Table 1). The first floras of California (Bolander 1865; Burt Davy 1901; Abrams 1911; Hitchcock 1912) identified the most common bunchgrass of the Central Valley, the foothills of the Sierra Nevada, and the Coast Ranges as *Stipa setigera*, which was first described from South American collections (Presl 1973). This is the name that Clements used in his early writings (Clements 1920; Clements and Weaver 1924; Weaver and Clements 1929). *Stipa setigera* was a widespread taxon, ranging over California, Oregon, New Mexico, Texas, and South America (Thurber 1880). Although considered variable (Thurber 1880), it was not until 1915 that taxonomists recognized that the name *Stipa setigera* had been misapplied to the California grass (Hitchcock 1915). Based on Presl's original description, it was clear that the name did not apply to the California species (Hitchcock 1915; Presl 1973) and, therefore, Hitchcock described the California bunchgrass as the new species *Stipa pulchra*, restricted to California and Baja California. Even though this new name was used in the floras of California as early as 1923 (Davidson and Moxley 1923; Hitchcock 1923), Clements did not start using it until 1934 (Clements 1934).

In 1941, it was recognized that the taxon *Stipa pulchra* consisted of two distinct types (Stebbins and Love 1941). The form that was predominant in the outer Coast Ranges and the wooded parts of the Sierra Nevada foothills retained the name *Stipa pulchra*, and the other form, occurring primarily in the treeless parts of the inner Coast Ranges, the southern part of the Central Valley and the valleys of southern California was described as *Stipa cernua*. Because Clements' important works on the California grasslands were published before 1941, all references that Clements made to *Stipa setigera* or *Stipa pulchra* did not distinguish these two new types.

A recent taxonomic treatment re-assigns all North American *Stipa* species to several other genera (Barkworth 1990). The most recent California flora accepts this treatment and moves *Stipa pulchra* and *Stipa cernua* into the genus *Nassella* (Barkworth 1993); *Stipa pulchra* becomes *Nassella pulchra* and *Stipa cernua* becomes *Nassella cernua*. This reclassification does not have the ecological ramifications that past nomenclatural changes have had, but it does change the taxonomic relationships of these California bunchgrasses to other North American species formerly considered to belong to the genus *Stipa*.

In this paper, I use species names as they are used by the author of the publication to which I am referring. In parenthesis after the name, I will include my interpretation of the name of the taxon following Barkworth (1993). Because pre-1941 publications did not recognize *Nassella pulchra* as distinct from *Nassella cernua*, I will interpret pre-1941 use of the name *Stipa pulchra* as *Nassella pulchra* sensu lato (s.l.). The name *Stipa setigera* was misapplied and re-

ferred to a number of different taxa; therefore, depending on the context I will either interpret it as *Nassella pulchra* (s.l.), or not attempt interpretation.

ORIGINS OF IDEAS CONCERNING THE PRE-EUROPEAN GRASSLANDS

When Clements first proposed that the pre-European vegetation of the Central Valley had been perennial grassland (Clements 1920), the decline and disappearance of native California bunchgrasses, precipitated by grazing of domestic livestock, had already been documented for parts of northwestern California (Burt Davy 1902). Clements, however, was the first to propose that perennial bunchgrasses had dominated the Central Valley and grassland areas of the central and south Coast Ranges. Although it had been known by at least 1880 that 'grassland' areas of California had come to be dominated by non-native grasses (Thurber 1880), descriptions of the Central Valley from the early 1990s did not distinguish between native and non-native grass taxa, or speculate on the nature of the pre-European vegetation. For example, even though *Avena fatua* (wild oat) was known by grass taxonomists to be non-native, one description by a major figure in California botany states that in the Central Valley "the herbaceous vegetation in aboriginal days grew with utmost rankness, so rank as to excite the wonderment of the first whites, who repeatedly tell of tying wild oats or grasses over the backs of their riding horses" (Jepson 1910).

In 1917, the Executive Committee of the Carnegie Institution of Washington (by which Clements was employed) decided that attention should be given to "grazing problems" (Clements 1917). In the course of this work, Clements studied the vegetation of many western states, including California (Clements 1917; Clements 1918; Clements 1919). This resulted in the first published descriptions of the presumed pre-European vegetation of the California Central Valley (Clements 1920).

Clements recognized that the original vegetation had long since disappeared, so he attempted to reconstruct the pre-European condition by searching out 'relict' patches of grasses. After deciding that the original dominants had been *Stipa setigera* (*Nassella pulchra* s.l.) and *Stipa eminens* (*Nassella lepida*), he searched for 'relict' patches to determine the extent of the original grassland. As a result, he concluded that these grasses had dominated the Central Valley from Bakersfield to Mount Shasta and from the foothills of the Sierra Nevada and Cascade mountains, through much of the Coast Ranges (Clements 1920).

Describing the 'grasslands' of California, Clements said that "the native bunch grasses once occupied all of the Great Valley of California as well as the valleys and lower foothills of the Coast and

Cross ranges and of the Sierra Nevada" (Weaver and Clements 1929). Nevertheless, such statements must be understood as describing what he perceived to be the potential vegetation that would develop in a given area based on the climate (Clements 1916). Clements recognized that the dominant species in an area at a given time would depend on hydrology and soil type. For example, he states that in parts of the San Joaquin, Salinas, and other valleys, species other than *Nassella pulchra* s.l., such as *Elymus triticoides* (= *Leymus triticoides*), formed extensive communities. He also described a "great complex of tule marshes" in the Sacramento and San Joaquin river delta (Clements and Shelford 1939).

WHAT WAS CLEMENTS' EVIDENCE?

By the time Clements became interested in what are now non-native-annual-dominated grasslands in California, the vegetation of these areas had been so extensively altered that the pre-European condition was unrecognizable. In his words, "the valleys and hills of California are to-day covered with a continuous mantle composed of annual species. . . . These have seemingly replaced the native perennials . . . so completely as to have produced grave doubt as to the composition of the original climax" (Clements 1934). Despite this, Clements harbored no doubt that he had correctly ascertained the pre-European vegetation: the "search for relict areas . . . has been so successful that it is now possible to determine its original area and composition . . ." (Weaver and Clements 1929). What was the evidence that Clements found so convincing?

In his first publication on the topic, Clements stated that "it was confirmed in 1917 . . . that *Stipa setigera* (*Nassella pulchra* s.l.) and *S. eminens* (*Nassella lepida*) were the original bunch-grasses of California" (Clements 1920), but he did not present data on which this conclusion was based. He continued "the [Californian] part of the [Pacific grasslands] is much more fragmentary, so much so in fact that it has had to be reconstructed from widely scattered relicts." Somehow Clements had convinced himself that scattered patches of *Stipa setigera* (*Nassella pulchra* s.l.) were relicts of a once vast association. For example, he used the occurrence of a few individuals of *Stipa setigera* (*Nassella pulchra* s.l.) growing among *Opuntia* near Banning, California, as evidence that "extensive areas" were once bunchgrass dominated (Clements 1934). He even used the occurrence of bunchgrasses in the deserts of California to conclude that these areas had once been bunchgrass prairie that had been transformed due to climatic changes (Clements 1920).

The primary observational evidence that Clements relied on was the vegetation along railroad right-of-ways in the Central Valley (Clements 1920). Along the tracks he observed "many hundred

miles of a nearly continuous consociation of *Stipa pulchra* (*Nassella pulchra* s.l.)” that was “often remarkable in purity and extent” (Clements 1934). Clements wrote that “it was especial good fortune to record these extensive relicts and then to have seen them reduced to patches here and there, as it . . . confirms the other evidence to the effect that grassland was the original great climax of California . . .” (Clements 1934).

Although Clements mentions “other evidence”, it is not clear to what he was referring. To determine the original extent of the perennial grasslands he made a “special search . . . for relict patches of *Stipa*” (Clements 1920), but there is no indication in any of his writings how he determined that these patches were relicts. Clements also maintained that he supplemented this search with “information from collections, ranges, the statements of early settlers, and the accounts of earlier collectors and explorers” (Clements 1920), but the only source he cites is a report by J. Burtt Davy that dealt with northwestern California and entirely different species of grasses (Burtt Davy 1902).

Many years later, Clements wrote that his conclusions were reinforced by field and garden studies although, again, he did not give any more information (Clements and Shelford 1939). I have been unable to find evidence for any experiments that Clements might have performed that could have supported his claims. In his book *Experimental Vegetation* (Clements and Weaver 1924), Clements reports planting *Stipa setigera* (*Nassella pulchra* s.l.) at a number of plots in the Midwest with the result that the California grass was always killed by winter weather. Clements never comments on the relevancy of this finding for determinations of the pre-European vegetation of California. I have found one other reference to a set of enclosure experiments performed at Palo Alto by a colleague of Clements, but the results never seem to have been published (Vestal 1929).

So we are left with the only evidence being widely scattered patches of *Stipa setigera* (*Nassella pulchra* s.l.) in the ‘grassland’ areas of California and fairly pure communities of this grass along trackways in the Central Valley. Clements did provide one major clue into his thinking, however, when he stated “The constant examination of fenced right-of-ways . . . has confirmed the *theoretical assumption* that this was formerly a vast *Stipa* association” (Clements 1920) (emphasis added). Fortunately, Clements has provided enough information in his writings to elucidate this suggestive statement.

CLIMAX THEORY AND THE CALIFORNIA GRASSLANDS

To understand how Clements came to the conclusion that *Stipa setigera* (*Nassella pulchra* s.l.) was the original dominant of Cali-

for California grasslands, it is necessary to understand the conceptual framework he had developed for vegetation analysis and the problems that he was interested in addressing. In his influential 1905 work *Research Methods in Ecology*, Clements laid the foundations of the theory that was to govern his career and the entire field of ecology in the United States for many years. He was looking for a "guiding principle" or "logical superstructure" on which to base the science of ecology, and, in his view, this principle was the relationship between "habitat" and plant. To Clements, this was a direct cause-and-effect relationship in which a "habitat" (i.e., various environmental factors) is the cause and plants and plant communities are the effects (Clements 1905). One of the primary research goals to which Clements applied his theory was in development of an explanation for continental-scale vegetation patterns of North America.

With his next major publication in 1916, Clements developed his ecological theory to the point that he viewed every successional sequence as ending in a definite, stabilized state called a formation or a climax (Clements 1916). His theory did allow for situations where conditions might greatly slow a successional sequence, but in general he viewed succession as the development and reproduction of a complex organism, and, as such, every successional sequence always eventually ended in a single, determinate state controlled by climate. Using his climax theory, Clements classified the vegetation of North America into 19 climaxes. He had not yet considered the 'grasslands' of California or the Palouse Prairie of the Pacific Northwest, but he concluded that the major grasslands of the Great Plains were one climax with three major plant associations.

By the publication of *Plant Indicators* in 1920, Clements no longer viewed his climax theory as a useful model nor as a hypothesis requiring testing, but as a fundamental principle:

... it is ... necessary to recognize that the successional areas in the great grassland formation, for example, are an integral part of the climax, however much they may differ from it. *Whatever seems inconsistent in this is apparent and not real*, since it is a matter of common knowledge that the same organism may appear in two or more unlike forms, such as the seedling and adult plant ... (Clements 1920).

He continued by stating the criteria by which climaxes could be 'objectively' recognized: (1) dominant plants must all belong to the same vegetation-form, (2) one or more of the dominant species must range throughout the formation as a dominant, (3) the majority of the dominant genera extended throughout the formation, (4) subclimax dominants give way to climax dominants through succession. In addition, it was a commonly accepted idea, which Clements had already stated in 1916, that, although annuals might dominate an

area in an early successional stage, they would typically yield to perennials in later stages (e.g., Clements 1916; Sampson and Chase 1927; Bews 1929; Piemeisel and Lawson 1937).

So consider Clements' conceptual framework and the issues in which he was interested when he came to California for his expeditions of 1917, 1918, and 1919. He was taking a large-scale, long-term view of community classification (Bartolome 1989). Following in the footsteps of other authors (Merriam 1898; Hall and Grinnell 1919), Clements wanted to understand large-scale vegetation patterns. In this pursuit, Clements was inclined toward a classification scheme with a few large categories rather than many small categories. He had already decided that the Great Plains were a single climax formation dominated by the genera *Stipa*, *Agropyrum* (= *Agropyron* sensu lato), *Bouteloua*, *Aristida*, and *Koeleria*. Based on the work of Weaver (1917), Clements concluded that the Palouse Prairie of the Pacific Northwest was part of the same climax. He had thus included all the grassland areas of North America in one large climax formation by the time he arrived in California. Based on the criteria he had laid down for climaxes, if the 'grasslands' of California were to be included in this climax, the original dominants had to be perennial grasses, belonging to one of the five genera that he had already delineated. Thus, when he arrived, he was predisposed to look for particular taxa. Although most native grasses were scarce, the perennial bunchgrass that he identified as *Stipa setigera* (*Nassella pulchra* s.l.) was common (Bolander 1865), and was the only one listed by other authors as an indicator species for certain climate zones in the state (Hall and Grinnell 1919). Guided by his theory, Clements knew a priori what he was looking for, and he found it.

Clements' hypotheses that (1) the California grasslands were dominated by *Stipa setigera* (*Nassella pulchra* s.l.) and (2) were part of a larger North American grassland climax would not have satisfied his own criteria for climax (particularly 2) if his putative dominant occurred only in California. However, because of a taxonomic mistake, he believed that the dominant grass in California was the widespread *Stipa setigera* instead of a California species with a much more restricted range. As already noted, the taxon *Stipa setigera* was considered to be distributed from San Diego County, northward to Oregon, eastward to New Mexico and Texas, and southward into South America (Thurber 1880; Hitchcock 1912). In fact, Clements used the occurrence of *Stipa setigera* and *Stipa emmens* (*Nassella lepida*) at high elevations of the mixed prairies in Texas and Arizona as evidence for the grassland climax (Clements and Weaver 1924). Clements assumed that the pre-European vegetation of those portions of California now dominated by introduced annual grasses formerly was native grassland. Then, in order to

group this 'grassland' with the other grasslands of North America, he needed the original dominants to be perennial grasses of certain genera. The occurrence of *Stipa* in California was the final piece of the puzzle that he needed:

The conclusion that the grassland is a single great climax formation is based in the first place on the fact that the three most important dominants, *Stipa*, *Agropyrum*, and *Bouteloua*, extend over most of the area, and one or the other is present in practically every association in it. This would seem the most conclusive evidence possible, short of actual vegetation experiments, that the grassland is a climatic vegetation unit (Clements 1920).

Clements was aware of the criticism that he was proposing the same climax for areas of California with vastly different amounts of rainfall. This criticism has, in fact, been used many times to argue against Clements' grassland hypothesis (e.g., Twisselmann 1967). His answer was that climate can only be recognized by vegetation: "No matter how complete his equipment of meteorological instruments, the ecologist must learn to subordinate his determination of climate to that of the plant . . ." (Clements 1920). Thus, he concluded that if dry areas such as the San Joaquin or Antelope Valley had bunchgrasses, then the climate was the same in these areas as in other areas with greater rainfall that supported bunchgrasses (Clements and Shelford 1939). The logic that he seemed to follow was that if two different areas both had bunchgrasses, then the climates were the same. If the climates were the same, then the climax vegetation was the same.

THE ACCEPTANCE OF THE PARADIGM

After Clements proposed his California grassland hypothesis in 1920, his ideas became so widely accepted as to form a standard paradigm. This paradigm consisted of two elements: (1) ideas concerning the composition and distribution of 'California bunchgrass grassland' and (2) the grouping of 'grasslands' in the entire Central Valley, the central and southern Coast Ranges, and southern California into a single community type.

In the almost eight decades since Clements first published his hypotheses, they have become widely accepted by researchers from a number of different areas. A major impetus to this acceptance was the publication in 1929 of Clements' textbook on ecology (co-authored with Weaver), that included his hypotheses on California vegetation (Weaver and Clements 1929). Thus began a trend in which his hypotheses were incorporated into textbooks in general ecology (e.g., Weaver and Clements 1938; Clements and Shelford 1939;

Oosting 1948; Oosting 1956; Shelford 1963; Barbour et al. 1987), general texts on grass taxonomy (e.g., Bews 1929; Gould 1968; Gould and Shaw 1983), range management (e.g., Stoddard et al. 1975), and fire ecology (e.g., Wright and Bailey 1982). The idea was reiterated in studies of California vegetation published in prestigious scientific journals such as *Ecology* (e.g., Klyver 1931; Clark 1937; Bentley and Talbot 1948). It was adopted by researchers at the United States Department of Agriculture (e.g., Shantz and Zon 1924; McArdle and Costello 1936; Piemeisel and Lawson 1937), various California state agencies (e.g., Burcham 1957; Barry 1972), and the University of California Agricultural Experiment Station (e.g., Robbins 1940; Sampson et al. 1951). The dominance of *Stipa pulchra* (*Nassella pulchra*) was proclaimed in standard floras of California (e.g., Munz 1959, 1974), specialized floras of California grasses (e.g., Crampton 1974), and general treatises on California vegetation (e.g., Barbour and Major 1977). It was incorporated into general geographical treatments of California (e.g., Hornbeck 1983; Miller and Hyslop 1983), general treatments of the vegetation of North America (e.g., Kuchler 1964; Sims 1988), and treatments on grasslands of the world (e.g., Heady et al. 1992).

A few of these publications have been particularly influential owing to timing, place of publication, or nature of the publication. For example, the adoption of Clements' views with essentially no modification for the *Atlas of American Agriculture* in 1924 (Shantz and Zon 1924) was the first step in cementing Clements' hypotheses in the scientific community. This was the citation that got the California grassland hypothesis into textbooks (e.g., Bews 1929) and U.S. Senate documents (e.g., McArdle and Costello 1936). The next particularly influential publication was a paper in *Hilgardia* by Beetle (1947). This often-cited paper reinforced the idea with a number of range maps that show perennial grass species covering the entire Central Valley. One review published in 1957 (Burcham 1957) was so influential that many subsequent authors relied on it as a primary source (e.g., Gould 1968; Barry 1972; Wright and Bailey 1982; Gould and Shaw 1983). This review also served to introduce the California grassland hypothesis into many popular accounts of the natural history of California (e.g., Dasmann 1965; Bakker 1971; Barry 1972; Bakker 1984; Dasmann 1988; Fradkin 1995). Finally, the publication that firmly cemented the California grassland hypothesis in the minds of both scientists and the public, because it serves as a primary starting point for the study of California vegetation, was the treatment by Heady in 1977 (reprinted in 1988) in *Terrestrial Vegetation of California* (Heady 1977). Heady wrote "*Stipa pulchra* [*Nassella pulchra*], beyond all doubt, dominated the valley grassland."

Clements' ideas have proven to be important in another respect.

His system of vegetation classification was based on observations of plants in the field and was a great improvement over climatically determined life-zones in common use at the time (Merriam 1898; Hall and Grinnell 1919; Jepson 1925). These systems, for example, placed the entire floor of the Central Valley and the California portion of the Sonoran Desert in the same category. Although Clements' hierarchical system could allow for intra-regional differentiation, because of his emphasis on the highest level of classification, he did not look for differences in communities from north to south or from coast to interior. In the decades following Clements, researchers either used Clements views in their descriptions of the California 'grasslands' (e.g., Shantz and Zon 1924; Piemeisel and Lawson 1937), or simply described the vegetation as "grass" and left it at that (e.g., Shreve 1927; Wieslander and Jensen 1946; Jensen 1947). Even earlier researchers who recognized that the north coast of California was composed of different species and should not be classified in the same vegetation type as the Central Valley did not differentiate plant communities within the Central Valley or in southern California (e.g., Clark 1937).

The defining paper in California plant community classification was that of Munz and Keck in 1949, with an addition in 1950 (Munz and Keck 1949; Munz and Keck 1950). In their community descriptions, they combined the ideas of scientists such as Jensen (1947), who recognized a single vegetation type termed "grass", with the floristic ideas of Clements (1920) and classified all the 'grassland' areas of the Central Valley, the Inner Coast Ranges, and of southern California as bunchgrass grassland ("Valley Grassland") dominated by *Stipa pulchra* (*Nassella pulchra*). In addition, they recognized another, more mesic, grassland community for northern coastal California (that they termed "Coastal Prairie").

This two-type classification was adopted in Munz's (1959) widely used flora and, with little modification, became the standard description of California 'grasslands' (e.g., Burcham 1957; Kuchler 1964; Barry 1972; Ornduff 1974; Cheatham and Haller 1975; Holland and Keil 1990). This blanket acceptance persisted despite the fact that rainfall varies over this area by more than 800 mm (Bentley and Talbot 1948), and even though there was a known difference in species distribution and abundance between the northern and southern Central Valley, and between the Central Valley and the Coast Ranges (Stebbins and Love 1941; Beetle 1947; Burcham 1957).

ALTERNATIVE HYPOTHESES TO THE BUNCHGRASS PRAIRIE

Because of the widespread acceptance of Clements' hypothesis, it might be assumed that there were no competing hypotheses; however, this is not the case. In fact, there are several alternatives that

date back almost as far as the publication of Clements' original idea in 1920. The first major alternative to Clements' grassland hypothesis was published only two years after Clements' hypothesis (Cooper 1922). In this model, the area of California with 250–760 mm of rainfall per year was dominated by sclerophyllous shrubs. Thus, the pre-European vegetation of large parts of the Coast Ranges, the foothills of the Sierra Nevada, and even the northern end of the Central Valley was proposed to have been chaparral. Areas with less than 250 mm of rainfall were considered deserts. It is noteworthy that this hypothesis was first derived under the paradigm of Clementsian climax theory and used exactly the same types of observations that Clements used: assumed relict patches of vegetation and eyewitness reports. The difference is that the second hypothesis recognized the possibility that areas currently dominated by grasses may, at one time, have been dominated by other vegetation types.

This hypothesis was extended by a number of researchers over the next several decades (Bauer 1930; Sampson 1944; Wells 1962; Naveh 1967; Keeley 1989). Also using assumed relicts as evidence, Bauer argued that in addition to the areas named by Cooper, much of the southern San Joaquin Valley had also been chaparral and not grassland (Bauer 1930). Others have come to similar conclusions. For example, in an extensive study of the relationship between vegetation type, substrate, and disturbance, Wells (1962) concluded that the original vegetation of the San Luis Obispo area was broad-sclerophyll forest on all types of substratum. In his view, anthropogenically caused fires (starting with native Americans and continuing with European settlers) and grazing eventually destroyed this forest, leading to the currently observed mosaic of grassland, shrubland, and forest. Wells predicted that continued destruction of the original forest would lead to the increased popularity of the grassland climax hypothesis: "... if the present conditions continue, one can hardly doubt that the hypothesis of a grassland climax will gain ascendancy as the contrary evidence disappears."

Researchers who explicitly rejected Clements' climax theory also came to the conclusion that modern non-native-annual-dominated grasslands had been dominated by chaparral. In a comparison of California with areas of the Mediterranean Basin, Naveh (1967) came to the same conclusion as Cooper. He concludes that "the probability of a climatic bunchgrass climax ... seems very low." Recently, a number of scientists have championed the idea that many areas of California 'grasslands' were once dominated by chaparral (Zedler et al. 1983; Freudenberger et al. 1987; Hunter and Horenshtein 1992; Keeley 1993).

The second major alternative hypothesis was proposed by Jepson, who suggested that the pre-European vegetation of the Central Valley was dominated by annual plants (Jepson 1925). Research at the

San Joaquin Experimental Range (Talbot et al. 1939; Talbot and Biswell 1942) indicated that 'native' annual grasses were an important part of the flora. This caused some researchers (Bentley and Talbot 1948) to conclude that annuals may have dominated some areas of the foothill grasslands (at the time, *Festuca megalura* (= *Vulpia myuros*), was thought to be a native annual), and even researchers who still accepted Clements' hypothesis admitted that the California 'grasslands' were unique in the number of native annuals (Beetle 1947). Research into the climatic conditions that favor annual plants over perennials has also tended to support the dominant role of annual plants (though not necessarily grasses) in some areas (Blumler 1984; Blumler 1992; Paula Schiffman in press).

The recognition that California has many native annual species has led to a number of variants of this hypothesis. For example, one proposal is that perennial grasses were the original dominants along the coast where conditions are most favorable for them, and native annuals were dominant in areas such as the lower foothills of the western slope of the Sierra Nevada (Biswell 1956). Another idea is that the floor of the Central Valley was a largely native annual grassland, with desert at the extreme southern end, but that at higher elevations perennial grasses were dominant (Twisselmann 1967; Frenkel 1970; Baker 1978). Others hypothesized that the annual vegetation on the floor of the valley was composed of herbaceous plants other than grasses (Piemeisel and Lawson 1937; Hoover 1970). Based partly on research into the interactions between the giant kangaroo rat (*Dipodomys ingens* Merriam) and *Nassella*, this is also the conclusion reached for parts of the Carrizo Plain in San Luis Obispo County (Schiffman 1994; Schiffman in press).

The third major counter-hypothesis is that vegetation is not controlled primarily by climate, but by soil characteristics. Thus, grasslands were found on deep soils, with different vegetation types on other soils (Shreve 1927). This hypothesis was supported by Robinson (1968, 1971) and independently by Keeley (1993), who concluded that *Stipa pulchra* (*Nassella pulchra* s.l.) was dominant in the Central Valley grassland and in the foothills of the Coast Ranges only on deep agricultural-type soils or heavy soils high in mineral nutrients. Well-drained sandy soils and those poor in mineral nutrients probably never supported such associations.

A CRITICAL ANALYSIS OF CLEMENTS' DATA

There are a number of important problems with the evidence used to support Clements' hypothesis. The first is taxonomy. The common native bunchgrass of California was originally identified as the widespread *Stipa setigera*. In part, Clements used the distribution of this species to support his idea of a grassland climax over this area.

When *Stipa pulchra* (*Nassella pulchra* s.l.) in California was recognized as a different species, this line of evidence was no longer valid. Clements, however, never mentioned this in any of his later publications. He simply replaced one name with another, without any discussion of the consequences that this taxonomic change had for his ecological theory or his California grassland hypothesis.

The second problem is that Clements considered roadsides and trackways to be undisturbed relict vegetation. In 1932, Clements' close colleague, Weaver, directly attacked using roadside vegetation to draw conclusions about the vegetation of larger areas (Weaver and Fitzpatrick 1932). Weaver concluded: "Along roadways and in right-of-ways certain species make a good showing. Their conspicuousness and abundance are often such as to lead one to believe that they are really important in the prairie proper In many cases these are found only sparingly, if at all, in the prairies" This was two years before Clements wrote his 1934 paper discussing the fundamental utility of roadside vegetation. There is no doubt that Clements knew of this criticism (the paper is cited in one of his books (Weaver and Clements 1938)), but Clements never addressed the issue. Furthermore, the *Stipa* (*Nassella*) communities along the trackways near Fresno that Clements used as the prime example of the pristine vegetation in California were burned every year (Biswell 1956), and therefore were not undisturbed relict patches.

The third problem concerns a misunderstanding of the role of fire in *Nassella* communities. Clements recognized that these communities were being burned, but he thought this destroyed them (Clements 1934). It is now known that fire often promotes *Nassella* and probably resulted in an increase in density (Sampson 1944; Jones and Love 1945; Biswell 1956; Ahmed 1983).

Finally, Clements took other people's work out of context. In his 1920 publication, Clements cites the work of Burt Davy (1902) to support his contention that native *Stipa* species were the pre-European grasses of the Central Valley. Burt Davy, however, was discussing only extreme northwest California, not the Coast Ranges nor the Central Valley, and he was referring to an entirely different species of *Stipa* (*Stipa lemmoni* = *Achnatherum lemmonii*)!

THE VIEW TODAY

We return to the question as to the nature of the pre-European vegetation that is dominated today by introduced annual grasses. In many areas, there is little question that the pre-European vegetation was oak forest, chaparral, or coastal sage scrub, as California has a well-documented history of shrub-clearing as a 'range improvement' practice (e.g., Sampson 1944; Jones and Love 1945; Arnold et al. 1951; Wells 1962; McKell et al. 1965; Zedler et al. 1983; Freuden-

berger et al. 1987; Huenneke 1989; Hunter and Horenstein 1992; Keeley 1993). For areas in northern California and in the northern part of the Central Valley, there are reliable eyewitness accounts of the existence of bunchgrasses (Burcham 1957; Wester 1981). In the way of physical evidence, microfossils in the form of silica bodies (opal phytoliths) most probably from *Nassella pulchra* have been found in areas of northern California that are today dominated by introduced annual grasses (Bartolome et al. 1986). Although strong evidence for the occurrence of *Nassella* in these areas, presence of these silica bodies does not preclude the possibility that the original vegetation was savanna or woodland.

Nassella pulchra is the most common native perennial grass today, and it is probable that in many areas it may have increased due to anthropogenic disturbances (Bartolome and Gemmill 1981). For example, *Nassella pulchra* is known to colonize road cuts (Clements 1934; Heady et al. 1992), and it is promoted by fire (Sampson 1944; Jones and Love 1945; Wells 1962; Ahmed 1983). Frequent burning can even be used to help produce monocultures of *Nassella pulchra* (Paul Kephardt, personal communication).

What can be concluded about the pre-European vegetation of the Central Valley? Eyewitness accounts from the early 1800s of the central and southern Central Valley appear inconclusive (Heady 1977). Wester has pointed out that most of the early accounts that mention bunchgrasses are from northern coastal locations or the Coast Ranges. Spanish and early Anglo-American accounts of the Central Valley (before serious overgrazing had occurred) tell of very sparse vegetation and no bunchgrasses. This might indicate that much of the southern Central Valley supported annual species. There are early accounts of bunchgrasses, but these descriptions confine bunchgrasses to the northeast portion of the San Joaquin Valley (Wester 1981).

There has never been any question that there were large areas of riparian vegetation and fresh water marshes around rivers (Shantz and Zon 1924; Clements and Shelford 1939; Burcham 1957; Heady 1977; Heady et al. 1992) and large vernal pool complexes on the eastern side of the Central Valley (Burcham 1957; Heady 1977; Heady et al. 1992). In addition, it is now generally agreed that areas of the valley floor, particularly in the southern Central Valley, are semi-desert (Twisselmann 1967; Menke 1989) and were originally dominated by some kind of desert scrub vegetation (Shantz and Zon 1924; Piemeisel and Lawson 1937; Burcham 1957; Twisselmann 1967; Heady 1977). This agrees with experimental work that found that the climate of the Kern Basin was too dry for perennial grasses (Jones and Love 1945).

Contemporary reviewers (Keeley 1989; Heady et al. 1992; Holland and Keil 1995) have tended to be much more careful in their

claims than those writing during the first eight decades of the century. The most recent reviews have tended to reverse the view of vast, relatively homogeneous perennial grasslands, and portray the pre-European California 'grassland' vegetation as a complex mosaic of different herbaceous communities with the particular species composition depending on climate and local conditions. Nobody has yet declared that perennial grasslands were unimportant components of California's vegetation, but there has been an increasing recognition that there are species differences and changes in relative abundance of perennials and annuals between north and south, Coast Ranges and Central Valley, and within the Central Valley depending on specific site conditions. With the recognition that *Vulpia myuros* is not native, as was once thought (Lonard and Gould 1974), many researchers have proposed that annual forbs filled the interstitial spaces of perennial grasslands, because there seem to be few common graminaceous candidates other than *Vulpia myuros* (Crampton 1974; Keeley 1989; Heady et al. 1992).

We will never know with certainty what the pre-European vegetation of large portions of California looked like. Nonetheless, the evidence strongly indicates that the poetic images of *Nassella*-dominated bunchgrass prairie blanketing vast expanses of the Central Valley and other 'grassland' areas of California are not accurate. There probably were stands of bunchgrasses in the northern Central Valley on rich soils and in some areas of the Coast Ranges. The central and southern Central Valley was probably a complex mosaic of plant communities with bunchgrasses becoming less and less important toward the south. In these areas, communities of annuals probably dominated, with forbs being more important than grasses. Finally at the extreme southern end of the Central Valley, a desert scrub vegetation probably dominated.

THE LEGACY OF CLEMENTS

Clements' California grassland hypothesis did not become the standard paradigm because it was based on the most convincing evidence or because there were no credible alternatives. The primary reason it became so widespread was because Clements was one of the most influential ecologists of the twentieth century. Clements' tremendous influence was due in great part to his voluminous writings on virtually every topic in ecology (Hagen 1992). In addition to research papers and monographs, Clements wrote or strongly influenced the standard textbooks of ecology for at least 35 years (Weaver and Clements 1929; Clements and Shelford 1939; Oosting 1956; Shelford 1963).

Clements continually ignored criticism or alternative hypotheses in his writings. For example, in other contexts, Clements cited Coo-

per's monograph that contains a directly contrary hypothesis concerning the California grasslands (Cooper 1922) but never addressed Cooper's ideas concerning that hypothesis. Because of Clement's silence concerning alternative hypotheses, much of the existing dissent was known only to a limited group of specialists.

Clements does not bear sole responsibility for the lack of recognition accorded alternative hypotheses. His paradigm was also perpetuated because important reviews downplayed alternatives (Burcham 1957; Heady 1977). Reviews can continue to perpetuate ideas after they are considered by other specialists in the field to be in doubt or even to be outdated.

Clements' legacy in ideas pertaining to grasslands in California has been far reaching. Today, we are still trying to shake off his influence. For example, the emphasis on *Nassella pulchra* as the dominant of large areas of 'grasslands' in California has led to concentration ecological research and restoration and management efforts on this species, at the expense of others. More studies, such as that of Dennis (1989), that compare the different effects of management regimes on a variety of native grasses are needed.

Because of the Clementsian paradigm that there were few north/south or coastal/interior differences in California grass communities, there has been a lack of appreciation for these differences. Management prescriptions developed in Jepson Prairie in northern California (Menke 1992) may not be appropriate for 'grassland' areas of southern California. It is only very recently that there has been a growing recognition that regional differences in 'grassland' communities, as well as ecotypic variation in native species, might be important ecologically (Huenneke 1989; Keeley 1989; Huntsinger et al. 1996). Community classifications that include more vegetation types may help in this regard (Thorne 1976; Holland 1986; Magney 1992), as may a more fine-scale floristic-based approach (Sawyer and Keeler-Wolf 1995).

Recognition that areas which today are dominated by annual grasses formerly may have been dominated by a different vegetation type (e.g., oak woodland, chaparral, or coastal sage scrub) can benefit restoration programs (Keeley 1993). With this recognition, potential sites for 'grassland' restoration can be chosen to allow true restoration, rather than type conversion. Also, an increase in shrubs in some areas may not be a call to action, because this may actually be recovery from past disturbance rather than an invasion of an endangered grassland community (e.g., McBride and Heady 1968).

Although simplification for popular publications is sometimes necessary and desirable, oversimplification is not. Popular references abound (e.g., Dasmann 1965; Barry 1972; Bakker 1984; Dasmann 1988; Edwards 1992; Fradkin 1995) that simply perpetuate Clements' ideas and do not incorporate the latest thinking. Lack of

appreciation of the diversity of California's plant communities can lead to poor decisions when questions of funding for basic research, conservation, or management are concerned. It is important that ecologists begin to convey to the public the complexity and diversity, rather than the homogeneity, of the vegetation.

The foregoing history is a reminder of the potential dangers of forcing facts to fit a hypothesis. It is true that, for observations to contribute to scientific knowledge, they must be influenced by theory; without any kind of conceptual framework with which to understand what we see, observations will be unintelligible (Kosso 1992). Nevertheless, hypotheses can also become traps if one forgets that the guiding hypothesis is only that, and is itself open to modification or replacement. Clementsian climax theory was a great advance for its time, but its widespread acceptance eventually hindered advance in ecology, conservation, and management. When Clements came to California, he used his theory to understand what he saw, but he, and many others, neglected to critically evaluate these views in light of all the evidence.

Because the observations of any individual are necessarily influenced by that person's preconceived notions, objectivity can only be achieved by subjecting ideas to the diverse community of scientists for debate (Pickett et al. 1994). Weight of authority should have no place in acceptance of scientific theories. Clements used his position as one of the preeminent ecologists of his day to promote his ideas. He ignored alternatives, and many other scientists chose not to discuss dissenting ideas. The consequences of this lack of open debate are still with us today.

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