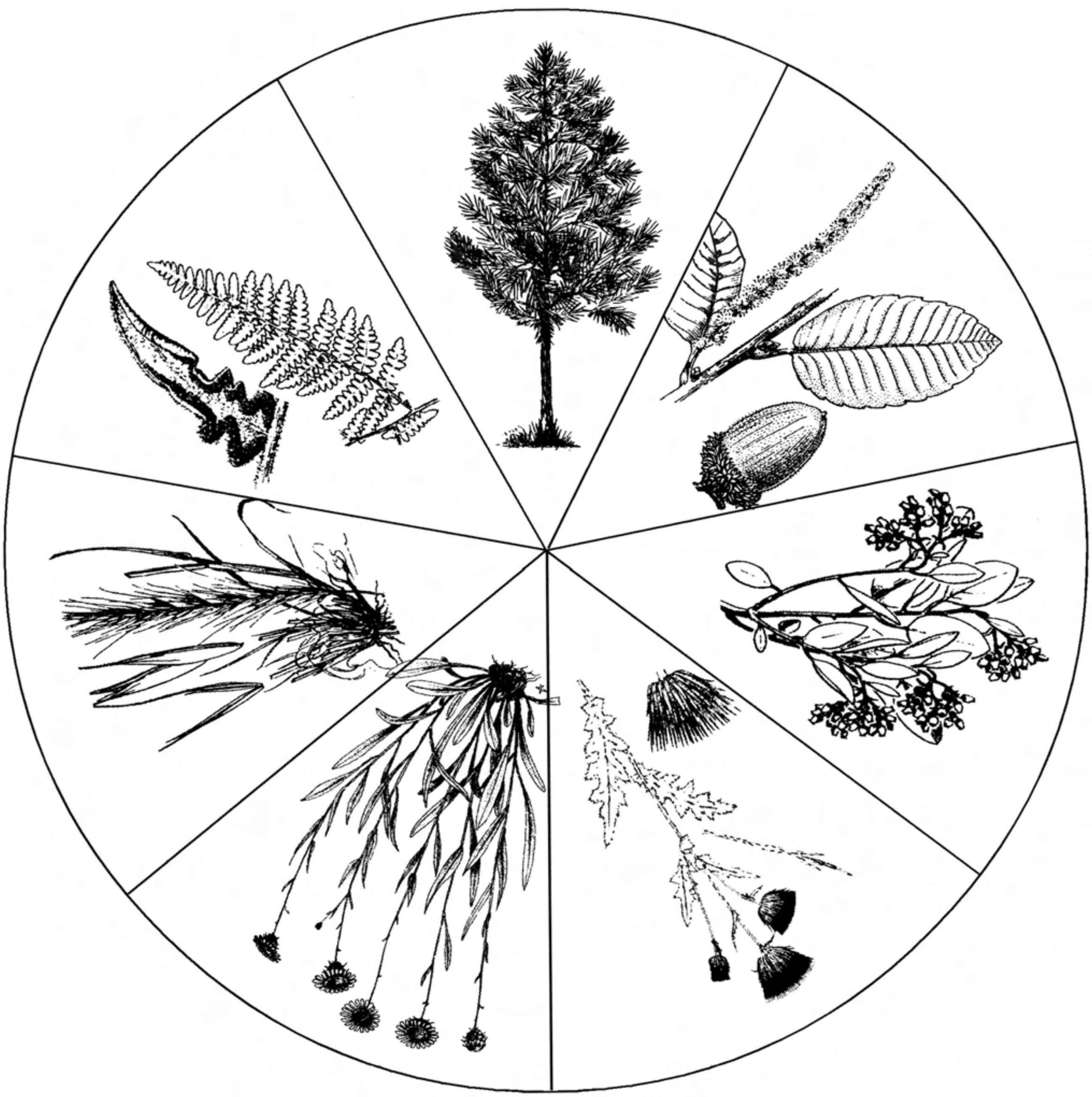
United States
Department
of Agriculture

Forest Service

**Pacific Southwest
Research Station**
http://www.psw.fs.fed.us/
Research Paper
PSW-RP-239

Diversity, Density, and Development of Early Vegetation in a Small Clear-cut Environment

Philip M. McDonald



Publisher:

Albany, California
Mailing address:
PO Box 245, Berkeley CA
94701-0245

510 559-6300

http://www.psw.fs.fed.us

September 1999

Pacific Southwest Research Station

Forest Service
U.S. Department of Agriculture

Abstract

McDonald, Philip M. 1999. **Diversity, density, and development of early vegetation in a small clear-cut environment.** Res. Paper PSW-RP-239. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 22 p.

On a high quality site in northern California, frequency, density, foliar cover, and height were measured on every plant species present in an 8-acre clear-cut opening each year from 1976 through 1980. Plant species numbered 71, although no more than 62 were present during a given year. Categories of vegetation with the most plants per acre initially were shrubs, annuals and biennials, and ferns; at the end of the study the categories were annuals and biennials, graminoids, and shrubs. At the beginning of the study, bracken fern provided the highest amount of foliar cover, whereas 5 years later shrubs and annuals and biennials provided the most cover. Hardwoods and graminoids were the tallest categories of vegetation. At the study's end density was 112,408 plants per acre, foliar cover was 17,433 ft^2 per acre and the tallest plants were 3.5 to 4.9 feet tall. Implications for future species development, plant succession, and community composition are presented.

Retrieval Terms: natural vegetation, northern California, plant community, plant species development, small forest opening

The Author

Philip M. McDonald is a research forester assigned to the Pacific Southwest Research Station's Forest Growth and Development Research Unit at the Silviculture Laboratory, 2400 Washington Ave., Redding, CA 96001.

Diversity, Density, and Development of Early Vegetation in a Small Clear-cut Environment

Philip M. McDonald

Pacific Southwest Research Station

USDA Forest Service
Research Paper
PSW-RP-239

September 1999

Contents

In Brief ... ii

Introduction ... 1

Methods ... 2
- Species and Site Characteristics ... 2
- Treatment, Measurement, and Analysis ... 4
- Sampling ... 4

Results ... 5
- Plant Diversity ... 5
- Individual Species ... 6
- Categories of Species ... 14
- The Plant Community ... 18

Discussion and Conclusions ... 19

References ... 22

In Brief...

McDonald, Philip M. 1999. **Diversity, density, and development of early vegetation in a small clear-cut environment.** Res. Paper PSW-RP-239. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 22 p.

Retrieval Terms: natural vegetation, northern California, plant community dynamics, plant species development, small forest opening

The forest ecosystem manager of the near future will need a tremendous amount of data. An inescapable fact is that an ecosystem cannot be managed without inventory data on as many plants, animals, insects, and genes as possible. Disturbance, either from nature or humans, is inevitable, and key questions include: how do ecosystems change and develop after a disturbance, and what are the long-term implications of such changes? Unfortunately, data to answer these questions are lacking or fragmented.

The primary focus of this 5-year (1976-1980) study was to record every plant species that was present in a small composite clearing on a high quality site in northern California and to measure the height and width of each over time. In addition, the five major regeneration strategies were examined to determine which were operative and to link species presence and development to them. Change was a major interest. The presence or absence of a species, the gain or loss in density, an elongation or decline in height—all were observed with interest. Further, the ascendence or decline of various categories of vegetation (conifers, hardwoods, shrubs, annuals and biennials, perennials, graminoids [grasses and sedges], and bracken fern) were monitored with vigor.

The fact that this was a high quality site is important. To the vegetation, this means plentiful rainfall, warm temperatures, and a long growing season. It also means deep soil, with inherent capability to catch and hold critical moisture. Further, it suggests that the nutrient pool is large and that critical nutrients are available as long as soil moisture is adequate. More specifically, it means that the land can support many plants of many species with a potential for rapid growth. However, the long, hot, rainless summers of the Mediterranean climate guarantee that when the soil moisture is gone, there is no more. Soil moisture is the limiting factor to establishment, growth, and survival. Plants must adapt a strategy of growing as fast as they can as soon as they can. Then they either die or find a way to endure months of high temperatures, searing winds, and minimum amounts of soil moisture.

Seventy-one species were present during this study. The number of plant species present after one growing season was 47 and after five seasons was 62. Nine species had disappeared by the study's end, only to be replaced by many new species, mostly perennials. Plant density reflected the high quality site with 24,860 plants per acre present initially and 112,408 per acre after five growing seasons. Foliar cover increased from 950 to 17,433 ft^2 per acre during the study, and the tallest plants were 3.5 to 4.9 feet in height. In general, the annuals and biennials were major contributors to density, shrubs to foliar cover, and the graminoids to height. For a given descriptor (density, cover, height), and specific year, many species excelled at least once. The most consistent ratings, however, were achieved by bracken fern, which ranked among the top four species each year in terms of density and foliar cover, and tanoak, which was present among the top four species in terms of height for 4 of the 5 years in the study.

All five regeneration strategies were used: rapid growth above ground was characterized by the root crown sprouts of the hardwoods and shrubs, rapid growth below ground by bracken fern, the seedling bank by tanoak and at least one perennial, windblown seeds by many annuals and biennials as well as graminoids and some perennials, and finally the seedbank in the soil by many shrubs and some annuals and perennials.

Some early trends in the composition of the future plant community can be deciphered. Chief among them were that initial species with tall life forms and either established root systems or capability to rapidly develop downward thrusting systems probably will do well. Hardwoods and shrubs have this capability and will dominate in the future plant community. The conifers, chiefly ponderosa pine, will also be present in the future community, but scattered as individual trees and in small aggregations. Shade-enduring perennials and bracken fern will be present in the understory of the future plant community; they also tend to develop deep and extensive root systems. The more shallow-rooted annuals and graminoids are likely to be represented only by small numbers in small openings where site resources are more readily available.

Introduction

As ecosystem management and the enhancement of forest health become applied to Federal forest land (Dombeck 1997, Salwasser 1992, Thomas 1994), information on the past, present, and future plant community will be invaluable. Small openings in the landscape that are created by wildfire, insect outbreak, or logging are commonplace, and knowledge is especially needed about them. Merchantable stems in these areas often are harvested, the slash disposed of, and the ground prepared for natural seeding or planting of desirable species.

Soil surfaces in these areas often are bare and temporarily devoid of most plants and animals. Available site resources, however, are high because large quantities of organic material are incorporated into the soil through harvesting and site preparation, and large amounts of moisture are absorbed by this organic matter. Warm temperatures and added moisture cause a rapid buildup of microorganisms that decompose organic material and liberate nutrients. Such nutrients, particularly nitrogen, increase on productive sites during the first year or two after site preparation and then decline precipitously (Smethhurst and Nambiar 1990).

In this fertile, but unstable and rapidly changing environment, the early plant community is dynamic—increasing rapidly in number of species and number of plants, but changing as plants of some species become numerous and those of other species decline. In productive environments, vegetative regrowth originates from five regeneration strategies: rapid growth above ground (as from sprouting hardwoods), rapid growth below ground (as from rhizomatous species), buried seedbanks in the soil (many shrub species), seedling banks (shade tolerant species), and windblown seeds (many annual species) (Grime 1979). In addition to the regeneration strategies, with their inherent considerations of plant morphology, structure, and propagule dispersion, many other factors influence plant location, density, and development in small openings on productive sites. These include slope and aspect, past community makeup, and dominance potential of the various species.

Secondary plant succession, which is concerned with the development of vegetation on temporarily-bare soil, was once thought of as primarily an orderly process (Clements 1916, Odum 1969). The first category of plants to become established after the soil was bared were the annuals, followed by the herbaceous perennials, then the shrubs, and eventually the trees. This sequence or set of stages was based on the precept that each category of vegetation prepared the way for the next stage through environmental modification. However, Egler (1954) suggested that succession was not necessarily an orderly or predictable process. Rather, the ensuing plant community developed from the propagules (seeds, rhizomes) initially present in the area. Margalef (1963) noted that the composition of early (pioneer) communities was determined by chance arrival during the initial period when competition was low. In this study, plants from buried seeds, rhizomes, and sprouts were already present and composition was hardly random. The impasse of orderly or random processes could be resolved by assuming that the future composition of many forest plant communities derives from a combination of both.

What is the process of plant succession in small openings surrounded by trees? How can it be determined when the very species in these openings are largely unknown? McDonald and others (1996) noted a major weakness when beginning ecosystem management on forested or formerly forested land: "very little is known about the shrubs, forbs, and grasses in the community" (p. 1). Gordon (1979) recommended that foresters begin to build a database for vegetation that is expected in specific areas. Wagner and Zasada (1991) stated that forest managers across North America need to consider the potential effect of noncrop vegetation on nearly every acre of newly forested land. These, of course, are the currently uneconomic (noncrop) species as opposed to the "valuable" (economic) conifers. O'Hara and others (1994) suggested that future forestry must embrace a mix of commercially valuable and nonvaluable species, and Rietveld (1992) noted an increased demand for diverse tree and shrub nursery stock, especially for species that provide food and shelter for wildlife.

The major objectives of this study were to ascertain the species composition of an early plant community in a small clear-cutting in the northern Sierra Nevada and to gain knowledge on early successional trends. More specific objectives were to list every species that was present in the clearing each year for 5 years after site preparation, and to determine each species' density and development, both alone and in such categories as conifers, hardwoods, shrubs, annuals and biennials, perennials, graminoids, and bracken fern. A second objective was to determine density and developmental trends in each of these categories.

Methods

Species and Site Characteristics

The study was located on the Challenge Experimental Forest in north central California (Yuba County, T19N, R7E MDM, Section 29). Site quality is high and the dominant species, ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), will average about 95 feet in height in 50 years (Powers and Oliver 1978). Other tree species scattered over the Forest are coast Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco), sugar pine (*Pinus lambertiana* Dougl.), California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), and incense-cedar (*Libocedrus decurrens* Torr.). Scientific and common names of trees are from Little (1979), scientific names of all vegetation other than trees is from Hickman (1993), and common names and plant symbols are from the U.S. Department of Agriculture (1994). Hardwoods, principally California black oak (*Quercus kelloggii* Newb.), (plant symbol *Quke*), tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.), (plant symbol *Lide3*), and Pacific madrone (*Arbutus menziesii* Pursh) (*Arme) (table 1*), are present throughout as individual trees, clumps, or groves. In terms of ecological subregions of California, the area corresponds to section M261E Sierra Nevada and the granitic and metamorphic hills subsection (U.S. Department of Agriculture 1997).

Table 1*—Scientific names, symbols, and common names of plant species in a composite clearcutting, Challenge Experimental Forest, 1976-1980*

Vegetation category	Scientific name	Plant symbol	Common name
Conifers	*Libocedrus decurrens*	*Lide*	Incense-cedar
	Pseudotuga menziesii var. *menziesii*	*PsmeM*	Coast Douglas-fir
	Pinus ponderosa var. *ponderosa*	*PipoP*	Ponderosa pine
Hardwoods	*Arbutus menziesii*	*Arme*	Pacific madrone
	Lithocarpus densiflorus	*Lide3*	Tanoak
	Quercus chrysolepis	*Quch2*	Canyon live oak
	Quercus kelloggii	*Quke*	California black oak
Shrubs	*Arctostaphylos mewukka*	*Arme3*	Indian manzanita
	Arctostaphylos viscida	*Arvi4*	Whiteleaf manzanita
	Baccharis pilularis	*Bapi*	Coyote brush
	Ceanothus lemmonii	*Cele*	Lemmon's ceanothus
	Ceanothus prostratus	*Cepr*	Squawcarpet
	Chamaebatia foliolosa	*Chfo*	Sierran mountain misery
	Garrya fremontii	*Gafr*	Bearbrush
	Haplopappus linearifolius	*Hali5*	Ericameria linearifolia
	Ribes roezlii	*Riro*	Sierran gooseberry
	Rosa gymnocarpa	*Rogy*	Dwarf rose
	Rubus glaucifolius	*Rugl*	Smoothleaf raspberry
	Toxicodendron diversilobum	*Todi*	Pacific poison oak
	Vitis californica	*Vica5*	California wild grape
Annuals and biennials	*Cirsium vulgare*	*Civu*	Bull thistle
	Clarkia rhomboidea	Clrh	Diamond fairyfan
	Conyza canadensis	*Coca5*	Canadian horseweed
	Collomia heterophylla	*Cohe2*	Variableleaf mtn. trumpet
	Epilobium paniculatum	*Eppa2*	
	Eremocarpus setigerus	*Erse3*	Turkey mullein
	Galium aparine	*Gaap2*	Stickywilly
	Gnaphalium luteo-album	*Gnlu*	Jersey cudweed
	Hypochaeris glabra	*Hygl2*	Smooth catsear
	Lactuca serriola	*Lase*	Prickly lettuce
	Lotus denticulatus	*Lode*	Riverbar birdfoot trefoil
	Lotus humistratus	*Lohu2*	Foothill deervetch
	Lotus purshianus	*Lopu3*	
	Madia gracilis	*Magr3*	Grassy tarweed
	Mimulus torreyi	*Mito*	Torrey's monkeyflower

continues

Trees on the Experimental Forest larger than 3.5 inches in diameter at breast height (d.b.h.) number more than 245 per acre and the average acre contains about 270 ft^2/acre of basal area. The previous forest was logged (at least for the largest and best trees) from about 1860 through 1890 (McDonald and Lahore 1984). Thus, logging and inevitable fire caused the current forest to be a mosaic of even-aged, second-growth stands, with the oldest dominant and codominant trees being more than 100 years and averaging about 140 feet tall. Trees 170 feet and taller at the same age are not unusual.

Trees in the dominant and codominant crown classes on the Experimental Forest average about 35 per acre, 70 percent of which are ponderosa pines. In general, many trees of the more shade-tolerant species (Douglas-fir, California white fir, incense-cedar, sugar pine, and tanoak) are younger, reflecting a decreasing incidence of fire in the area. Greenleaf manzanita (*Arvi4*), deerbrush (*Cein3*), and western bracken fern (*Ptaq*) are common on the Forest and often become abundant *(table 1)*. Poison oak (*Todi*) is ubiquitous and abundant, and grows equally well in sun and shade environments.

Herbivores, chiefly deer *(Odocoileus* spp.*)*, woodrats *(Neotoma* spp.*)*, and deer mice *(Peromyscus maniculatus)*, are plentiful throughout the Experimental Forest.

Summers on the Forest are hot and dry; winters cool and moist. The average midsummer maximum temperature, based on 43 years of record, is 90 °F; the midwinter minimum is 30 °F. The

***Table 1**, continued*

Vegetation category	Scientific name	Plant symbol	Common name
Annuals and biennials	*Sonchus asper*	*Soas*	Spiny sowthistle
	Stephanomeria virgata	*Stvi2*	Rod wirelettuce
	Tragopogon dubius	*Trdu*	Yellow salsify
	Trifolium ciliolatum	*Trci*	Foothill clover
	Vicia americana	*Viam*	American vetch
	Viola lobata	*Vilo2*	Moosehorn violet
Perennials	*Agoseris grandiflora*	*Aggr*	Bigflower agoseris
	Apocynum pumilum	*Appu*	
	Aster radulinus	*Asra*	Roughleaf aster
	Campanula prenanthoides	*Capr15*	
	Convolvulus aridus	*Coar11*	
	Dichelostemma capitatum	*Dica14*	Bluedicks
	Eriophyllum lanatum	*Erla6*	Woolly eriophyllum
	Fragaria vesca	Frve	Woodland strawberry
	Galium bolanderi	*Gabo*	Bolander's bedstraw
	Horkelia tridentata	*Hotr*	Threetooth honeydew
	Hypericum concinnum	*Hyco3*	Goldwire
	Hypochaeris radicata	*Hyra3*	Hairy catsear
	Iris hartwegii	*Irha*	Rainbow iris
	Osmorhiza chilensis	*Osch*	
	Polygala cornuta	*Poco4*	Sierran milkwort
	Potentilla glandulosa	*Pogl9*	Gland cinquefoil
	Sanicula graveolens	*Sagr5*	Northern sanicle
	Sidalcea malvaeflora	*Sima2*	Dwarf checkermallow
	Tauschia kelloggii	*Take*	Kellogg's umbrellawort
	Trientalis latifolia	*Trla6*	
	Unknown rosette	*Unkn*	
Graminoids	*Bromus* (unknown)	*Br*sp	
	Bromus orcuttianus	Bror2	Orcutt's brome
	Carex (unknown)	*Ca*sp	
	Elymus glaucus	*Elgl*	Blue wildrye
	Festuca myuros	*Femy2*	
	Festuca occidentalis	*Feoc*	Western fescue
	Sitanion hystrix	*Sihy*	
Bracken fern	*Pteridium aquilinum* var. *pubescens*	*Ptaq*	Western bracken fern

growing season is about 200 days. Average annual precipitation is 68 inches with 94 percent falling between October and May. Soil moisture is the limiting factor and drought the primary cause of mortality for most plants. The Aiken soil grades from loam to clay-loam texture with depth, and is deep, moderately well drained, and quite fertile. The study area, located at the 2,750-foot elevation, faces southwest and has a 20 percent slope.

Treatment, Measurement, and Analysis

Merchantable trees were harvested in two small clear-cuttings in 1975, and slash and unmerchantable trees were piled with a bulldozer in windrows and burned in the fall *(fig. 1)*. Very little soil was placed in the windrows. The clear-cuttings were 8.0 and 7.75 acres in size and about one-fourth of a mile apart. Their soil, slope, aspect, and vegetation were representative of much of the Experimental Forest. The two clear-cuttings were similar in every respect with one exception—most abundant shrub species. In spring 1976, large numbers of whiteleaf manzanita (*Arvi4*) seedlings were present in one opening; deerbrush (*Cein3*) seedlings in the other. Although not a trace of either species remained above ground, large numbers of both species from dormant, but viable, seeds in the soil were expected in each opening. The difference between openings was not anticipated. However, as noted by Sousa (1984) and others, the environment within a patch cleared by disturbance is seldom, if ever, homogeneous. Different microsites are inevitable and slightly different plant communities will become present in each because of the adaptation of particular colonists to each. Because the overall geographical features, soil, and vegetation were similar, data from the two openings were combined as a composite to more closely represent this environment on the Experimental Forest.

Sampling

Sampling took place in the fall along three randomly selected diagonal transects in each opening that roughly represented the top, middle, and bottom of each. Because the opening boundaries were irregular, the length of the transects varied. Beginning and ending points of each transect were clearly marked. Ten sampling locations were evenly distributed along each and determined by pacing. Sample locations included the edge environment within 10 feet of the forest, but not burned windrows or riparian vegetation in ephemeral stream channels near the bottom of the openings. Each location became the center of a circular milacre (0.001 acre) plot. These were not permanently marked, and thus the location of the plots varied slightly each year.

All vegetation was measured on each plot each year from 1976 through 1980. Years of extreme drought were 1976 and 1977; 1978 was extremely wet, and 1979 and 1980 were about normal. Each plant species was sampled for density, foliar cover, and height. Density was defined as the number of

Figure 1—A portion of the study area on the Challenge Experimental Forest in 1976. Close examination shows a few small plants scattered throughout the opening.

plants on each milacre plot expanded to a per-acre basis. Foliar cover was an estimate of the sum of shadows that would be cast by leaves and stems of individual species expressed as a percentage of the land surface (Daubenmire 1968). It is an expression of horizontal development. For each species, amounts greater than 0.5 ft^2 were recorded to the nearest 1.0 ft^2 and less than this value as a trace (T). If a plant leaned into the milacre and had at least a square foot of foliar cover in it, it was given a density value of one plant. Plant height was denoted as "average dominant" and defined as the average of the three tallest stems measured from mean groundline to bud. The height of an outward leaning plant was recorded where it crossed the plot boundary. Frequency also was determined to provide an estimate of species distribution within the opening. It was defined as the number of plots having one or more plants of a given species divided by the total number of plots and expressed as a percent.

Results

Plant Diversity

A total of 71 plant species was found during the 5-year study (*table 1*), although no more than 62 species were present during a given year (*table 2*). At the beginning of the study, the 45 species in the plant community consisted of 0 conifer seedlings; 3 hardwoods from both root-crowns and seeds, 11 shrubs, mostly from buried seeds; 15 annuals and biennials, all from seeds; 15 perennials, almost all from seeds; 2 graminoids (grasses and sedges), from seeds; and bracken fern, from rhizomes. At the end of the study, the 62 species in the plant community consisted of 3 conifers, 2 hardwoods, 12 shrubs, 20 annuals and biennials, 18 perennials, 6 graminoids, and bracken fern (*table 2; fig. 2*). All categories of vegetation increased, except hardwoods and fern, for an overall gain in diversity of 32 percent.

Table 2*—Plant species diversity by vegetation category in a composite clearcutting, Challenge Experimental Forest, 1976-1980*

Year	Conifers	Hardwoods	Shrubs	Annuals	Perennials	Graminoids	Fern	Total
				Number of species				
1976	0	3	11	15	15	2	1	47
1977	3	2	12	16	12	7	1	53
1978	3	3	11	18	14	7	1	57
1979	3	2	12	16	15	6	1	55
1980	3	2	12	20	18	6	1	62

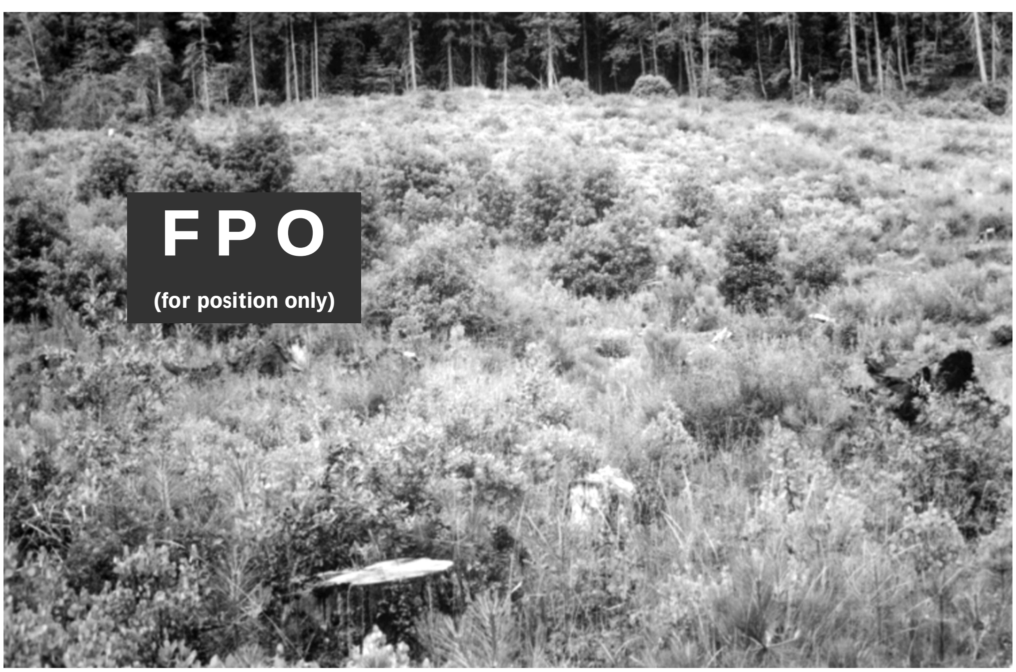


Figure 2—At the end of the study in 1980, the land was rapidly becoming clothed with many plants from several categories of vegetation, Challenge Experimental Forest, 1980.

Individual Species

The vast majority of species became established early and persisted throughout the study period. Several species, however, invaded early, were present for 1 to 3 years, and then disappeared. These included Pacific madrone (*Arme*), bearbrush (*Gafr*), turkey mullein (*Erse3*), threetooth honeydew (*Hotr*), canyon live oak (*Quch2*), northern sanicle (*Sagr5*), and *Sitanian hystrix (Sihy) (table 3).* They represented almost all the vegetation categories in the study. Other species invaded later in the study. Notable were coyote brush *(Bapi), Convolvulus aridus* (*Coar11*), woolly eriophyllum *(Erla6)*, Bolander's bedstraw (*Gabo*), Jersey cudweed (*Gnlu*), goldwire (*Hyco3*), *Osmorhiza chilensis (Osch*), and yellow salsify *(Trdu*), which, with one exception, were perennials.

Descriptive characteristics such as frequency, density, foliar cover, and height of the 71 plant species portray the distribution, density, and development trends of individual species over the 5-year study (*table 3*). Together, they encompass a wide variety of density and developmental trends, reactions to competition, and adaptations to micro-environments. Strategies to dominate in some way at key times also were observed. When the top four species in each descriptive characteristics class (density, cover, height) were ranked, their regeneration and development strategies became more clear (*table 4*). The first year after site preparation (1976), species like tanoak (*Lide3*), western bracken fern (*Ptaq*), and Pacific poison oak (*Todi*), which derived energy from parent root systems, dominated in terms of density and horizontal development (foliar cover). The second year (1977) was characterized by the addition of annuals like bull thistle (*Civu*) and American vetch (*Viam*) and shrubs like whiteleaf manzanita (*Arvi4*) and deerbrush (*Cein3*) that originated mostly from windblown seeds or from dormant seeds in the soil. Year 3 (1978) was characterized by annuals like *Civu*, prickly lettuce (*Lase*), and American vetch that originated mostly from newly produced seeds, and shrubs such as deerbrush and whiteleaf manzanita that were developing rapidly. Species of note in year 4 (1979) were additional annuals like smooth catsear (*Hygl2*) and riverbar birdfoot trefoil (*Lode*) along with the above shrubs and western bracken fern (*Ptaq*). In year 5 (1980), density and cover were divided among most of the species in year 4 plus blue wildrye (*Elgl*) and tanoak (*Lide3*). Of particular note was western bracken fern, which was present among the top four species in both density and cover every year of the study. This was the only species to do this.

***Table 3**—Characteristics of individual species as they regenerated and developed during the study period, Challenge Experimental Forest, 1976-1980*

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Conifers	*Cade*	1976	-	-	-	-	-	-	-
		1977	5	67	33	T	0	0.2	0.1
		1978	2	17	0	T	0	0.5	0
		1979	3	33	0	T	0	0.5	0.4
		1980	2	17	0	T	0	0.6	0
	PsmeM	1976	-	-	-	-	-	-	-
		1977	2	17	0	T	0	0.2	0
		1978	3	33	0	T	0	0.6	0
		1979	3	33	0	T	0	0.4	0.2
		1980	5	50	0	T	0	0.6	0.4
	PipoP	1976	-	-	-	-	-	-	-
		1977	25	467	29	T	0	0.2	0.1
		1978	33	483	15	17	0	0.3	0.1
		1979	35	433	10	67	0	0.7	0.2
		1980	22	350	21	33	0	1.0	0.3
Hardwoods	*Arme*	1976	-	-	-	-	-	-	-
		1977	2	33	0	T	0	0.3	0
		1978	2	17	0	T	0	1.4	0
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-

continues

Table 3, continued

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Hardwoods	*Lide3*	1976	1	210	10	90	2	1.4	0.2
		1977	22	233	6	217	2	2.6	0.3
		1978	17	183	10	217	6	2.0	0.4
		1979	17	217	15	783	145	4.8	0.5
		1980	25	350	16	900	117	4.9	0.6
	Quch2	1976	1	10	0	10	0	0.4	0
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-
	Quke	1976	4	40	0	T	0	0.4	0.1
		1977	10	150	22	100	100	1.5	0.4
		1978	3	83	150	T	0	0.5	0.1
		1979	5	100	100	17	0	0.7	0.3
		1980	10	100	0	168	233	2.2	1.0
Shrubs	*Arme1*	1976	2	17	0	T	0	0.1	0
		1977	3	17	0	T	0	0.1	0
		1978	2	17	0	T	0	0.1	0
		1979	5	33	0	33	0	1.8	0.1
		1980	3	33	0	T	0	0.3	0.1
	Arvi4	1976	41	1,680	100	70	0	0.3	0.1
		1977	50	3,517	243	617	51	0.7	0.1
		1978	58	2,917	142	1,383	73	1.2	0.1
		1979	70	3,533	142	2,083	16	1.3	0.2
		1980	65	4,467	146	4,183	153	2.4	0.2
	Bapi	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	2	17	0	T	0	3.2	0
	Cein3	1976	60	2,960	550	T	0	0.2	0.1
		1977	63	3,150	580	717	20	1.2	0.1
		1978	63	3,783	125	1,850	68	1.4	0.1
		1979	72	3,000	46	4,100	114	2.3	0.2
		1980	67	2,617	47	4,033	106	3.4	0.4
	Cele	1976	9	360	138	10	0	0.2	0.1
		1977	10	533	219	100	58	0.5	0.1
		1978	7	417	214	150	100	0.7	0.1
		1979	17	1,250	225	800	134	0.9	0.1
		1980	8	683	553	583	585	1.2	0.4
	Cepr	1976	15	180	14	T	0	0.1	0.1
		1977	17	300	33	50	0	0.2	0.1
		1978	23	400	18	150	13	0.2	0.1
		1979	15	183	15	100	20	0.2	0.1
		1980	22	467	44	283	51	0.2	0.1
	Chfo	1976	16	630	73	80	14	0.5	0.1
		1977	13	800	243	167	87	0.5	0.1
		1978	18	750	118	117	24	0.5	0.1
		1979	27	2,517	215	550	68	0.8	0.1
		1980	22	2,267	301	283	48	0.7	0.1
	Gafr	1976	9	140	29	T	0	0.2	0.1
		1977	13	200	38	17	0	0.4	0.1
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-

continues

Table 3, continued

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Shrubs	*Hali5*	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	3	33	0	17	0	1.3	0.7
		1979	2	17	0	T	0	0.7	0
		1980	5	67	33	33	0	1.7	0.4
	Riro	1976	7	80	14	T	0	0.4	0.1
		1977	2	17	0	T	0	0.3	0
		1978	5	50	0	T	0	0.7	0.1
		1979	3	33	0	T	0	0.4	0.4
		1980	5	67	33	100	0	2.7	0.4
	Rogy	1976	14	430	60	30	0	0.4	0.1
		1977	10	417	91	83	67	0.6	0.1
		1978	17	1,133	255	67	100	0.5	0.1
		1979	12	367	116	33	T	0.7	0.1
		1980	13	350	56	T	0	0.6	0.1
	Rugl	1976	29	430	38	30	0	0.3	0.1
		1977	20	483	61	117	48	0.6	0.3
		1978	32	817	82	167	11	0.6	0.1
		1979	27	500	39	217	75	0.4	0.1
		1980	30	583	22	200	24	0.8	0.1
	Todi	1976	65	2,810	440	90	18	0.4	0.2
		1977	63	3,083	86	500	16	0.8	0.1
		1978	48	1,767	48	100	0	0.7	0.1
		1979	65	2,567	54	500	22	0.8	0.1
		1980	63	2,733	72	483	22	1.5	0.2
	Vica5	1976	-	-	-	-	-	-	-
		1977	2	17	0	T	0	0.5	0
		1978	-	-	-	-	-	-	-
		1979	2	17	0	T	0	0.4	0
		1980	-	-	-	-	-	-	-
Annuals and biennials	*Civu*	1976	49	1,860	67	110	43	0.6	0.2
		1977	88	20,367	367	1,833	41	1.5	0.1
		1978	95	13,583	216	2,467	66	1.7	0.2
		1979	70	3,467	73	467	21	1.6	0.1
		1980	62	4,017	55	267	27	1.6	0.1
	Clrh	1976	2	0	0	T	0	1.0	0.4
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	3	933	999	33	0	1.5	0.5
		1980	3	750	250	100	200	2.5	0.5
	Coca5	1976	-	-	-	-	-	-	-
		1977	3	50	50	17	0	2.8	1.0
		1978	7	67	0	T	0	1.9	0.6
		1979	3	50	50	T	0	1.1	0.2
		1980	7	1,083	441	17	0	0.7	0.4
	Cohe2	1976	1	90	0	T	0	0.3	0
		1977	8	950	229	T	0	0.3	0.1
		1978	17	2,183	244	83	67	0.4	0.1
		1979	-	-	-	-	-	-	-
		1980	10	817	539	T	0	0.3	0.1
	Eppa2	1976	-	-	-	-	-	-	-
		1977	3	100	0	T	0	1.8	0.7
		1978	13	717	266	50	50	2.1	0.3
		1979	20	600	81	T	0	1.4	0.1
		1980	42	3,500	244	67	0	1.7	0.2

continues

Table 3, continued

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Annuals and biennials	*Erse3*	1976	3	30	0	T	0	0.1	0.1
		1977	2	183	0	T	0	0.3	0
		1978	2	183	0	T	0	0.1	0
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-
	Gaap2	1976	-	-	-	-	-	-	-
		1977	2	17	0	T	0	0.5	0
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	2	17	0	T	0	3.1	0
	Gnlu	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	12	133	14	17	0	0.3	0.2
		1979	17	533	118	67	33	1.6	0.3
		1980	15	317	75	67	33	1.8	0.4
	Hygl2	1976	11	180	28	T	0	0.1	0.1
		1977	13	183	38	17	0	0.9	0.1
		1978	53	2,833	106	183	31	0.9	0.1
		1979	38	4,600	281	250	24	0.7	0.1
		1980	47	17,367	912	783	72	0.8	0.1
	Lase	1976	4	60	50	T	0	1.4	0.4
		1977	37	2,350	205	133	100	1.3	0.1
		1978	62	10,050	386	533	76	1.6	0.2
		1979	60	9,717	536	367	114	1.4	1.4
		1980	7	11,517	311	267	22	1.4	0.1
	Lode	1976	4	580	998	T	0	0.7	0.3
		1977	2	1,167	0	167	0	1.0	0
		1978	18	8,033	999	467	242	0.9	0.1
		1979	5	4,100	999	283	650	0.7	0.1
		1980	7	3,467	999	250	550	0.8	0.1
	Lohu2	1976	1	10	0	T	0	0.1	0.1
		1977	-	-	-	-	-	-	-
		1978	8	483	114	T	0	0.3	0.1
		1979	-	-	-	-	-	-	-
		1980	5	567	684	T	0	0.3	0.1
	Lopu3	1976	9	540	251	T	0	0.2	0.1
		1977	7	250	48	T	0	0.3	0.1
		1978	10	1,700	900	17	0	0.4	0.1
		1979	20	3,200	644	100	20	0.3	0.1
		1980	3	667	0	T	0	0.3	0
	Magr3	1976	2	50	50	T	0	0.9	0.7
		1977	5	67	33	T	0	1.1	0.5
		1978	10	883	539	83	0	2.1	0.1
		1979	12	833	338	33	0	1.6	0.2
		1980	38	4,500	387	250	47	2.1	0.1
	Mito	1976	12	480	246	T	0	0.1	0.1
		1977	8	283	166	T	0	0.3	0.1
		1978	12	1,433	525	17	0	0.3	0.1
		1979	7	833	617	T	0	0.5	0.1
		1980	15	817	172	T	0	0.5	0.1
	Soas	1976	10	130	21	T	0	0.1	0.1
		1977	3	50	50	17	0	1.7	1.6
		1978	8	367	163	33	0	1.6	0.4
		1979	5	50	0	T	0	0.8	0.3
		1980	8	167	77	T	0	1.0	0.3

continues

Table 3, continued

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Annuals and biennials	*Stvi2*	1976	-	-	-	-	-	-	-
		1977	7	850	762	133	100	1.6	0.7
		1978	18	500	100	50	50	1.5	0.2
		1979	12	250	55	T	0	1.7	0.2
		1980	23	3,533	999	200	0	2.4	0.4
	Trdu	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	3	33	0	T	0	1.4	0.1
		1979	2	17	0	T	0	1.0	0
		1980	2	17	0	T	0	2.2	0
	Trci	1976	1	10	0	T	0	0.2	0
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	3	217	350	T	0	0.3	0
	Viam	1976	44	2,610	104	10	0	0.2	0.1
		1977	48	5,183	262	317	46	0.4	0.1
		1978	53	10,000	408	233	29	0.3	0.1
		1979	48	3,467	217	117	24	0.6	0.1
		1980	47	7,450	433	400	99	0.7	0.1
	Vilo2	1976	11	170	31	T	0	0.1	0.1
		1977	10	117	17	T	0	0.2	0.1
		1978	17	500	86	T	0	0.4	0.1
		1979	7	183	55	T	0	0.2	0.1
		1980	7	233	65	T	0	0.4	0.1
Perennials	*Aggr*	1976	6	60	0	T	0	0.7	0.6
		1977	7	67	33	T	0	0.8	0.1
		1978	8	233	71	17	0	1.3	0.2
		1979	12	200	57	33	0	1.3	0.1
		1980	38	1,800	80	133	14	1.3	0.1
	Appu	1976	2	20	0	10	0	0.2	0
		1977	2	67	0	17	0	0.5	0
		1978	3	83	150	T	0	0.6	0.1
		1979	2	17	0	T	0	0.3	0
		1980	3	83	150	17	0	0.8	0.4
	Asra	1976	8	220	105	10	0	0.6	0.1
		1977	7	133	100	T	0	0.8	0.2
		1978	12	417	157	67	33	1.4	0.3
		1979	12	800	443	33	0	0.8	0.1
		1980	13	317	38	33	0	1.1	0.3
	Capr5	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	5	33	0	T	0	0.6	0.3
		1979	-	-	-	-	-	-	-
		1980	7	100	50	T	0	1.6	0.2
	Coar11	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	2	150	350	T	0	0.4	0
		1979	-	-	-	-	-	-	-
		1980	5	167	0	T	0	0.6	0.2

continues

Table 3, continued

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Perennials	*Dica14*	1976	2	30	50	T	0	0.2	0.1
		1977	2	17	0	T	0	0.9	0
		1978	-	-	-	-	-	-	-
		1979	5	50	0	T	0	1.6	0.1
		1980	5	67	33	T	0	1.2	0.1
	Erla6	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	2	17	0	T	0	0.5	0
		1980	2	50	0	T	0	1.3	0
	Frve	1976	6	180	97	T	0	0.2	0.1
		1977	2	117	0	T	0	0.2	0
		1978	7	100	29	T	0	0.3	0.1
		1979	-	-	-	-	-	-	-
		1980	2	117	0	T	0	0.2	0
	Gabo	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	10	200	37	30	0	0.5	0.1
		1979	20	417	47	67	0	0.4	0.1
		1980	23	450	34	117	17	0.7	0.1
	Hotr	1976	2	40	100	T	0	0.1	0.1
		1977	3	33	0	T	0	1.0	0
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-
	Hyco3	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	2	167	0	33	0	2.3	0
		1980	-	-	-	-	-	-	-
	Hyra3	1976	3	260	717	T	0	0.1	0.1
		1977	-	-	-	-	-	-	-
		1978	7	67	0	17	0	0.9	0.1
		1979	15	400	107	17	0	0.9	0.1
		1980	22	1,400	124	T	0	0.7	0.1
	Irha	1976	18	280	180	T	0	0.3	0.1
		1977	5	67	33	T	0	0.5	0.1
		1978	8	133	40	T	0	0.5	0.1
		1979	25	300	11	83	0	0.7	0.1
		1980	12	167	30	17	0	0.4	0.1
	Osch	1976	-	-	-	-	-	-	-
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	-	-	-	-	-	-	-
		1980	2	17	0	T	0	0.5	0.1
	Poco4	1976	4	90	48	T	0	0.2	0.1
		1977	3	67	100	T	0	0.4	0.1
		1978	7	83	25	T	0	0.5	0.1
		1979	7	200	200	17	0	0.5	0.1
		1980	2	17	0	T	0	0	0

continues

***Table 3**, continued*

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Perennials	*Pogl9*	1976	5	80	40	T	0	0.2	0.1
		1977	10	283	48	33	0	0.9	0.2
		1978	10	467	102	33	0	0.5	0.1
		1979	12	550	111	67	0	1.0	0.2
		1980	13	450	169	83	25	0.9	0.2
	Sagr5	1976	1	40	0	T	0	1.5	0.2
		1977	2	17	0	T	0	0.2	0
		1978	2	17	0	T	0	0.6	0
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-
	Sima2	1976	30	980	75	20	0	0.1	0.1
		1977	20	900	125	183	15	1.1	0.1
		1978	33	1,067	55	233	24	0.8	0.1
		1979	23	867	113	150	58	0.7	0.1
		1980	23	517	41	83	25	0.9	0.2
	Take	1976	4	70	48	T	0	0.4	0.2
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	3	33	0	T	0	0.7	0.2
		1980	3	50	50	T	0	0.8	0.2
	Trla6	1976	14	770	241	T	0	0.1	0.1
		1977	20	783	115	T	0	0.2	0.1
		1978	30	2,967	156	50	0	0.2	0.1
		1979	23	2,133	277	50	0	0.2	0.1
		1980	47	6,467	268	67	0	0.3	0.1
	Unkn	1976	1	10	0	T	0	0.2	0.1
		1977	-	-	-	-	-	-	-
		1978	-	-	-	-	-	-	-
		1979	2	17	0	T	0	0.4	0
		1980	2	17	0	T	0	0.3	0
Graminoids	Brsp	1976	-	-	-	-	-	-	-
		1977	17	1,100	327	217	98	2.7	0.1
		1978	20	1,983	290	150	18	1.8	0.3
		1979	7	2,383	999	500	409	3.1	0.1
		1980	7	900	999	250	650	2.9	0.4
	Bror2	1976	8	170	99	10	0	0.8	0.1
		1977	5	267	233	33	0	2.5	0.1
		1978	13	1,167	458	83	67	2.1	0.4
		1979	23	2,467	285	300	69	2.6	0.2
		1980	1	1,167	446	133	41	3.5	0.2
	Casp	1976	23	1,000	112	20	0	0.5	0.1
		1977	23	1,100	145	83	33	1.0	0.2
		1978	28	583	41	100	29	1.1	0.1
		1979	17	350	47	117	24	1.2	0.1
		1980	22	333	27	100	0	1.1	0.2
	Elgl	1976	-	-	-	-	-	-	-
		1977	3	33	0	T	0	1.6	1.3
		1978	15	3,817	999	267	260	2.1	0.5
		1979	12	1,950	541	150	0	3.1	0.4
		1980	57	8,400	319	800	77	2.8	0.3

continues

***Table 3**, continued*

Vegetation category	Species abbrev.	Year	Freq.	Density		Cover		Height	
			Pct	*Plants/acre*		*Ft²/acre*		*Ft*	
				Value	SE	Value	SE	Value	SE
Graminoids	*Femy2*	1976	-	-	-	-	-	-	-
		1977	2	17	0	T	0	0.4	0
		1978	2	750	0	17	0	1.2	0
		1979	7	500	307	17	0	1.0	0.2
		1980	8	317	73	T	0	0.9	0.1
	Feoc	1976	-	-	-	-	-	-	-
		1977	5	500	379	100	58	2.5	0.4
		1978	5	300	451	17	0	2.9	0.4
		1979	5	1,550	999	267	219	2.6	0.2
		1980	12	4,917	999	583	369	2.5	0.3
	Sihy	1976	-	-	-	-	-	-	-
		1977	2	17	0	T	0	0.5	0
		1978	2	100	0	T	0	1.0	0
		1979	-	-	-	-	-	-	-
		1980	-	-	-	-	-	-	-
Bracken fern	*Ptaq*	1976	47	3,760	73	350	12	0.8	0.1
		1977	57	10,233	173	1,367	34	1.0	0.2
		1978	65	10,333	265	1,517	107	1.0	0.3
		1979	47	8,133	248	1,283	39	1 0	0.1
		1980	52	7,883	229	1,067	49	1.1	0.1

***Table 4**—Top four plant species having largest number (density), best horizontal development (foliar cover), and best vertical development (height), Challenge Experimental Forest, 1976-1980*

Year	Rank	Density	Cover	Height
1976	1	*Ptaq*	*Ptaq*	*Sagr5*
	2	*Cein3*	*Civu*	*Lide3*
	3	*Viam*	*Lide3*	*Lase*
	4	*Todi*	*Todi*	*Clrh*
1977	1	*Civu*	*Civu*	*Coca5*
	2	*Ptaq*	*Ptaq*	*Brsp*
	3	*Viam*	*Cein3*	*Lide3*
	4	*Arvi4*	*Arvi4*	*Feoc*
1978	1	*Civu*	*Civu*	*Feoc*
	2	*Ptaq*	*Cein3*	*Bror2*
	3	*Lase*	*Ptaq*	*Elgl*
	4	*Viam*	*Arvi4*	*Magr3*
1979	1	*Lase*	*Cein3*	*Lide3*
	2	*Ptaq*	*Arvi4*	*Elgl*
	3	*Hygl2*	*Ptaq*	*Brsp*
	4	*Lode*	*Cele*	*Feoc*
1980	1	*Hygl*	*Arvi4*	*Lide3*
	2	*Lase*	*Cein3*	*Bror2*
	3	*Elgl*	*Ptaq*	*Cein3*
	4	*Ptaq*	*Lide3*	*Bapi*

Average dominant height, which is a measure of vertical development, was expressed best by tanoak (*Lide3*) in 1976 and a few plants of annual species that grew tall in the absence of competition. Height development from 1977 through 1979 was notable for a species of brome (*Brsp*), western fescue (*Feoc*), Orcutt's brome (*Bror2*), and blue wildrye (*Elgl*)—all perennial grasses—whose strategy was to grow tall at an early age. The tallest species in 1980 were a mixture of hardwood *(Lide3),* graminoid *(Bror2),* and such shrubs as deerbrush *(Cein3*) and coyote brush (*Bapi*). Of particular note was tanoak, which ranked among the four tallest species in 4 of the 5 years in the study.

One factor that can influence the density and horizontal development of plant species in newly developed openings is damage from biotic and abiotic agents. The only agent in this study that had a noticeable effect was deer. Browsing damage in fall 1976 to the young plants was severe. Species like deerbrush (*Cein3*) and California black oak (*Quke*) were browsed to nubs of naked stems, and larger perennials like dwarf checkermallow (*Sima2*) and gland cinquefoil (*Pogl9*) were virtually stripped of all green material. Most remarkable was that species like western bracken fern (*Ptaq*), Sierran mountain misery (*Chfo*), whiteleaf manzanita (*Arvi4*), Pacific poison oak (Todi), rainbow iris (*Irha*), and smoothleaf raspberry (*Rugl*), which are scarcely touched when older, were severely browsed. Even they became palatable, probably because of their high nutrient content—a response to the large amount of soil nitrogen available just after site preparation. Many plants of American vetch (*Viam*) were pulled out of the ground. Browsing declined rapidly in 1977 and rated only as occasional thereafter.

Categories of Species

Conifers

Conifer seedlings originated from seeds blown in from nearby trees in fall 1976. The most abundant species was ponderosa pine (*PipoP*). Mean conifer seedling density decreased from 551 to 417 per acre during the study (*fig. 3*). Horizontal and vertical development were slow, with values of 33 ft^2 per acre (*fig. 4*) and 0.7 foot (*fig. 5*), respectively, at the end of the study.

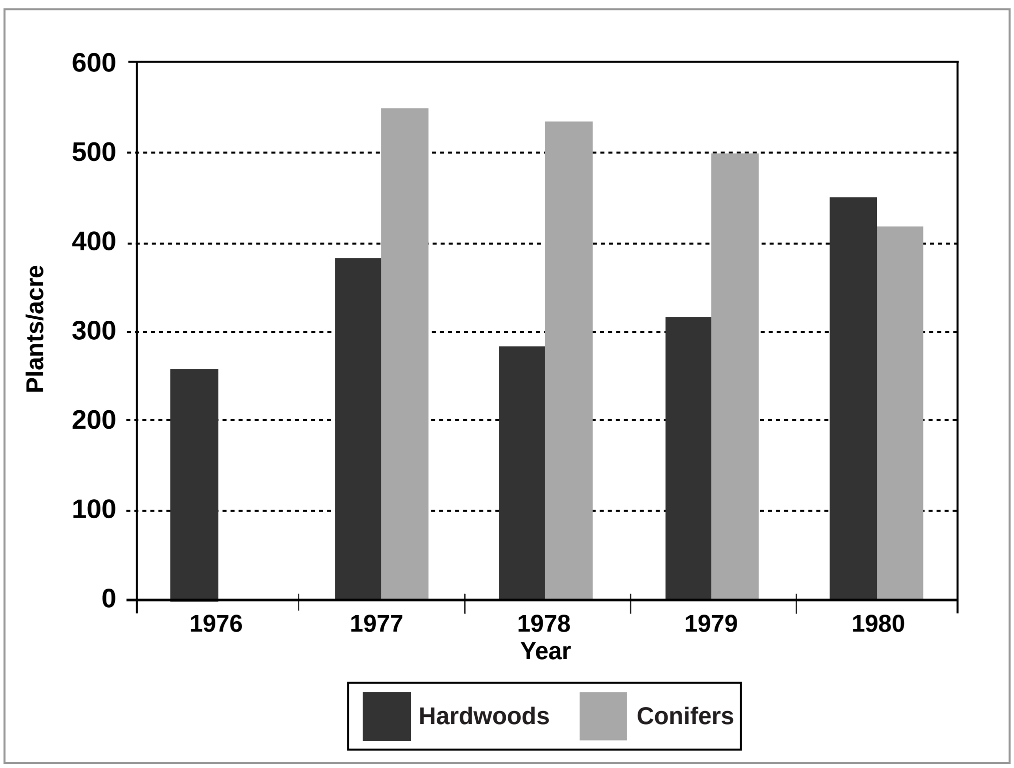


Figure 3—Density of hardwoods and conifers, Challenge Experimental Forest, 1976-1980. Standard errors for hardwoods ranged from 48 to 125 plants per acre in a given year; for conifers, from 80 to 153 plants per acre.

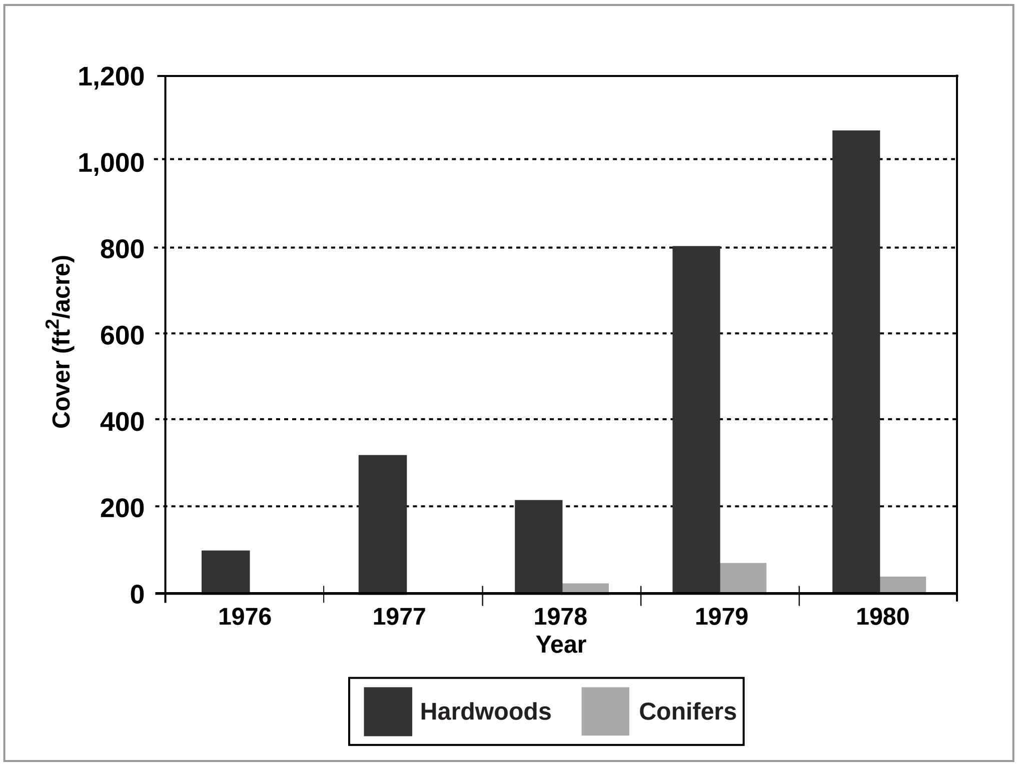


Figure 4—Foliar cover of hardwoods and conifers, Challenge Experimental Forest, 1976-1980. Standard errors for hardwoods ranged from 28 to 383 ft^2 per acre in a given year; for conifers, from 5 to 22 ft^2 per acre.

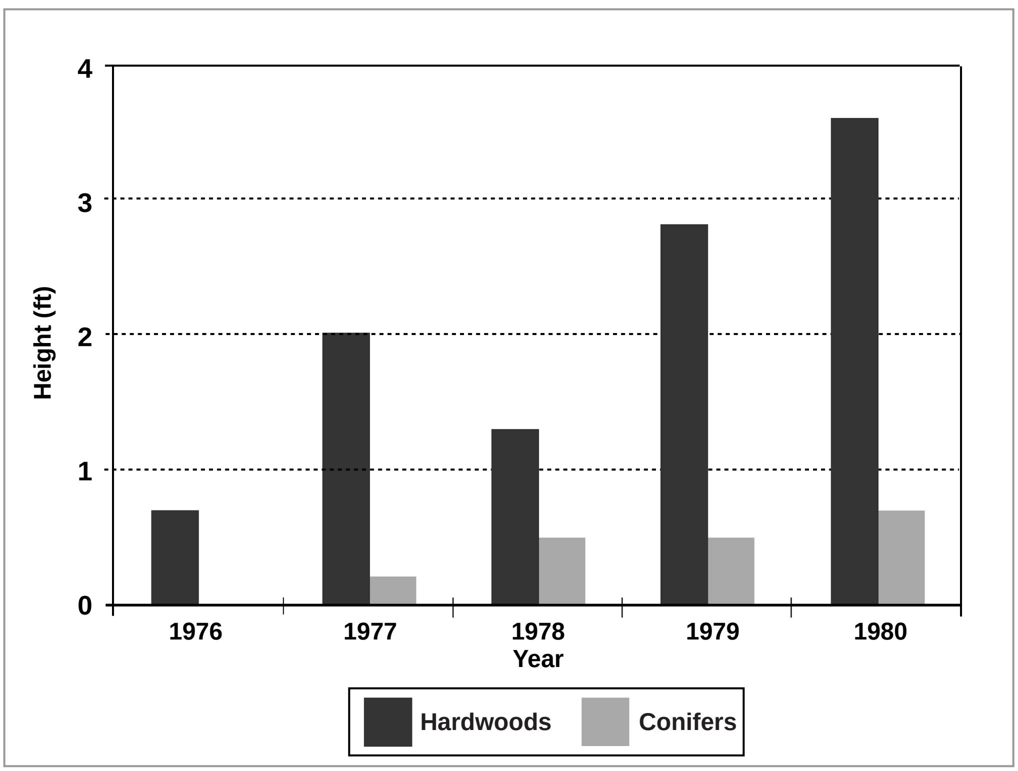


Figure 5—Height of hardwoods and conifers, Challenge Experimental Forest, 1976-1980. Standard errors for hardwoods ranged from 0.3 to 2.0 feet in a given year; for conifers, from 0 to 0.1 foot.

Hardwoods

Hardwoods initially were from two kinds of sprouts: root-crown sprouts that originated from dormant buds on the burl and seedling-sprouts. Seedling-sprouts, most of which were tanoak (*Lide3*), are resprouts of seedlings in the seedling bank that survived the harvest and site preparation, died back to groundline, and resprouted. Additional recruits to the hardwood category were by seedlings from acorns and berries. The few Pacific madrone (*Arme*) plants present in 1977-1978 were all from seed. The major contributor to the hardwood category was tanoak, which at the end of the study, was developing rapidly and forming tall, wide clumps of stems. During the study, hardwood density increased 73 percent (*fig. 3*), foliar cover expanded more than ten times (*fig. 4*), and height increased more than five times (*fig. 5*).

Shrubs

Plants from almost all species in this category were from seed. The one exception was Pacific poison oak (*Todi*), which originated from plants that escaped harvest and site preparation. Mean shrub density was characterized by a relatively high initial density (9,710 plants per acre) and a steady increase to 14,351 plants per acre at the end of the study (*fig. 6*), for a 48 percent gain. Foliar cover of shrubs expanded from 310 ft^2 per acre at the beginning to 10,181 ft^2 per acre at the end of the study for over a thirtyfold increase (*fig. 7*). Mean shrub height increased from 0.3 feet in 1976 to 1.6 feet in 1980 for more than a fivefold increase (*fig. 8*). Major contributors to these gains were whiteleaf manzanita (*Arvi4*), deerbrush (*Cein3*), Sierran mountain misery (*Chfo*), and Pacific poison oak (*Todi*). Deerbrush in particular was developing rapidly and forming large clumps of tall stems.

Annuals and Biennials

Plants in this category originated mostly from windblown seeds or from dormant seeds in the soil. Some species, notably bull thistle (*Civu*), developed first from windblown seed and then from seed of the ensuing plants. In contrast, plants of American vetch (*Viam*) originated from buried seed with subsequent recruitment from buried seed and seed produced by the plants. In terms of huge numbers of plants present soon after disturbance, both species were equally successful.

The classical buildup and decline of a biennial invader was illustrated by bull thistle (*Civu*), whose seeds blow in on the wind, germinate in the fall, result in plants that overwinter as a rosette,

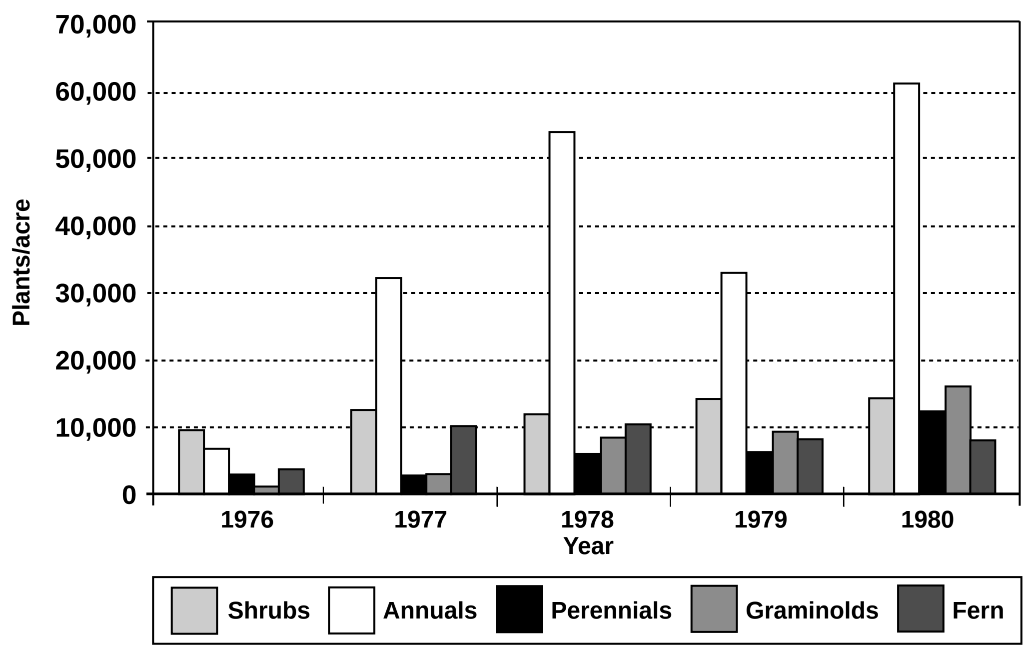


Figure 6—Density of five categories of vegetation, Challenge Experimental Forest, 1976-1980. Standard errors for shrubs ranged from 350 to 421 plants per acre in a given year; for annuals, from 197 to 1,268; perennials, from 74 to 360; for graminoids, from 92 to 489 plants per acre.

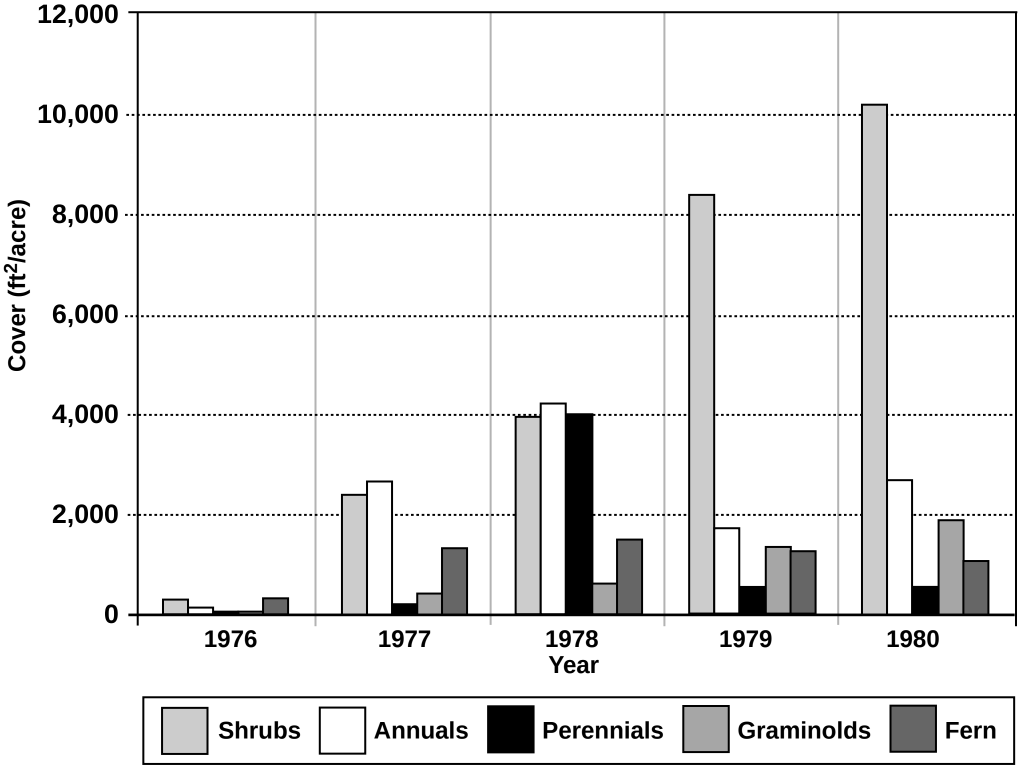


Figure 7—Foliar cover of five categories of vegetation, Challenge Experimental Forest, 1976-1980. Standard errors for shrubs ranged from 11 to 443 ft^2 per acre in a given year; for annuals, from 7 to 144; perennials, from 2 to 17; and for graminoids, from 5 to 128 ft^2 per acre.

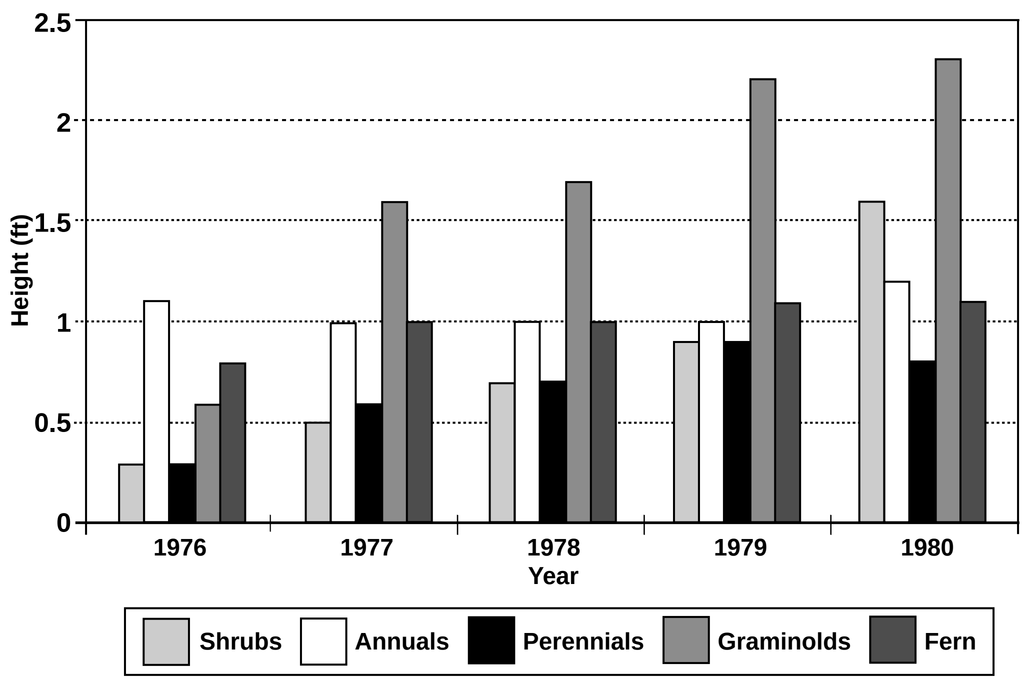


Figure 8—Height of five categories of vegetation, Challenge Experimental Forest, 1976-1980. Standard errors for shrubs ranged from 0.1 to 0.3 foot in a given year; for annuals, from 0.1 to 0.2; perennials, from 0.1 to 0.2; and for graminoids, from 0.2 to 0.4 foot.

bolt in early spring, grow tall, produce thousands of seeds, and die. The population peaked in 1977 and 1978, and then typically collapsed (*table 3*) (McDonald and Tappeiner 1986, Randall 1990). Plants of other species from all but the hardiest of propagules had a difficult time becoming established in these years (*fig. 9*).

The density of annuals and biennials began with fairly high numbers, increased almost fivefold by the end of 1977, and again increased (67 percent) in 1978 (*fig. 6*). Almost a 39 percent decrease characterized 1979 as the mean density of bull thistle (*Civu*), riverbar birdfoot trefoil (*Lode*), and American vetch (*Viam*) fell dramatically. Over 60,000 plants per acre were present in this category in 1980 due largely to increases in density by many species, including *Epilobium paniculatum* (*Eppa2*), smooth catsear (*Hygl2*), prickly lettuce (*Lase*), grassy tarweed (*Magr3*), rod wirelettuce (*Stvi2*), and American vetch (*Viam*). Foliar cover peaked in 1978 at 4,233 ft^2 per acre and declined to 2,668 ft^2 per acre in 1980 (*fig. 7*). Mean height of annuals and perennials ranged from 0.4 feet to 1.2 feet during the study (*fig. 8*).

Perennials

Most perennial species in this study originated from both seeds blown in on the wind or those from the seedbank in the soil. For the first 4 years, density was dominated by dwarf checkermallow (*Sima2*) and *Trientalis latifolia* (*Trla6*) and then in 1980 by *Trla6*, bigflower agoseris (*Aggr*), and hairy catsear (*Hyra3*) (*fig. 6*). Dwarf checkermallow also was a major contributor to foliar cover during the first 4 years, with bigflower agoseris and Bolander's bedstraw (*Gabo*) contributing most in 1980 (*fig. 7*). The tallest perennials were composed of different species almost every year and ranged from 0.1 to 1.5 feet tall in year 1 to 0.3 to 1.6 feet in 1980 (*fig. 8*).

Graminoids

When the study began, the graminoids consisted of one grass (Orcutt's brome [*Bror2*]) and one sedge (*Casp*). Together, their density was 1,170 plants per acre. This value increased steadily, so that by the end of the study the density of the six graminoids was more than 16,000 per acre (*fig. 6*). Foliar cover likewise increased steadily from 30 ft^2 per acre to 1,866 ft^2 per acre at the study's end (*fig. 7*). Mean height increased from 0.6 to 2.3 feet during the study (*fig. 8*).

Bracken Fern

Western bracken fern (*Ptaq*) is found from the Arctic Circle to the Equator and is common on every continent (Minore 1966). It is particularly adapted to disturbed areas, but retains a presence in all stages of succession. The density of this species began fairly high (3,760 stems per acre), increased dramatically to more than 10,200 stems per acre in 1977, flattened out in 1978 (10,333 per acre), and then declined the next 2 years (*fig. 6*). At the end of the study, bracken fern density was 7,883 stems per acre. Foliar cover began at 350 ft^2 per acre, increased through three growing seasons to 1,517 ft^2 per acre, and then declined to 1,067 ft^2 per acre at the end of the study (*fig. 7*). Mean height began at 0.8 foot and increased slowly to 1.1 feet at the study's end (*fig. 8*).

The Plant Community

Density of all plant species was 24,860 plants per acre after one growing season, increased through the third growing season to 91,631 plants per acre, declined the fourth season to 71,167 per acre, and then increased to 112,408 plants per acre at the end of the study. Foliar cover increased each year from 950 ft^2 per acre to 17,433 ft^2 per acre at the study's end.

When each category of species is presented for each descriptive characteristic and illustrated as a proportion of the total of that characteristic each year, the changing nature of the plant community is more apparent (*figs. 10, 11*).

On the virtually bare ground representative of the study area in fall 1976, the shrubs, annuals and biennials, and ferns dominated in terms of number of plants (*fig. 10*). By 1977, more than half of all the plants in the total community were annuals and biennials—a condition that continued throughout the study. Another category whose members increased in density throughout the study was the graminoids. Density of the conifers and hardwoods was very low compared to the other categories of vegetation. Density of shrubs and bracken fern declined proportionally as components of the plant community.

In terms of foliar cover (*fig. 11*), the initial values were largest for bracken fern, shrubs, and annuals and perennials, and continued as such for the next 2 years. In 1979, foliar cover of the

Figure 9—With over 20,000 thistles per acre using available resources, most other plant species would find it difficult to become established. Challenge Experimental Forest, 1977.

graminoids became larger than that of the fern. The large increase in shrub cover was also notable in 1979 when it amounted to more than 59 percent of that in the total plant community—a proportion that continued in 1980. In the last 2 years of the study, foliar cover of the hardwoods and graminoids was increasing, and that of the perennials was low and virtually stable. Foliar cover of the annuals and biennials was characterized by a buildup in 1977 and 1978, followed by a major decline in 1979, and a slight increase in 1980. The proportion of foliar cover contributed by the conifers was very low.

Of the species present during the study, 31 percent never had more than 0.5 ft^2 of cover. Conversely, after the first year, less than 25 percent of the species present contributed over 90 percent of foliar cover.

In terms of height, and by definition "average dominant height," all categories of vegetation were increasing over time except the perennials (*fig. 8*). Average dominant height, of course, is lowered by shorter new recruits, especially in instances where only one or two plants are present. Although many species indicated a propensity to grow tall during the study (*table 3*), only one category of vegetation, the graminoids, consistently dominated over all others in terms of vertical development *(fig. 8)*. The graminoids were also among the four tallest species present in 1977 through 1980 (*table 4, fig. 8*). Indeed, in 1978 and 1979, three of the four tallest species in the study were graminoids. Although the graminoids were taller, their height was leveling off (*fig. 8*). In contrast, the trend of shrub height not only was increasing, but at an increasing rate (*fig. 8*).

Discussion and Conclusions

Before harvest, the study area was covered with a dense mixture of conifer and hardwood trees of many sizes and age classes, including seedlings and saplings of shade tolerant species. The soil surface was mostly a dense carpet of needles and leaves with western bracken fern (*Ptaq*) and Pacific poison oak (*Todi*) scattered throughout. Sierran mountain misery (*Chfo*) also was present in scattered patches. After harvest and site preparation, the study area consisted of mostly bare ground with small tanoak (*Lide3*) and California black oak (*Quke*) stumps and residual plants of Pacific poison oak and Sierran mountain misery above ground and western bracken fern (*Ptaq*) below ground, along with thousands of dormant seeds in the soil.

These species, plus many more with plants from buried seeds and seeds that blew in on the wind, quickly invaded the study area. By the end of the first growing season, several categories of vegetation, including shrubs, annuals, ferns, and grasses, were well represented. None of these categories contained less than 7,800 plants per acre or a cover of less than 1,000 ft^2 per acre at the end of the study. The hardwoods also had a foliar cover of over 1,000 ft^2 per acre.

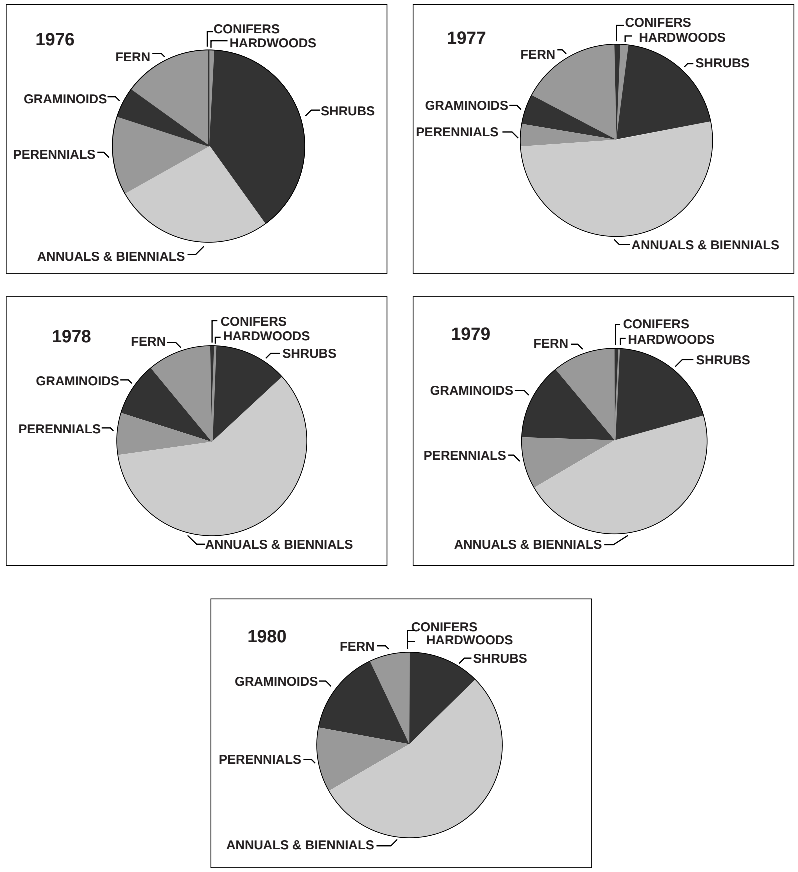


Figure 10—Proportional changes in plant density for the various categories of vegetation. Challenge Experimental Forest, 1976-1980.

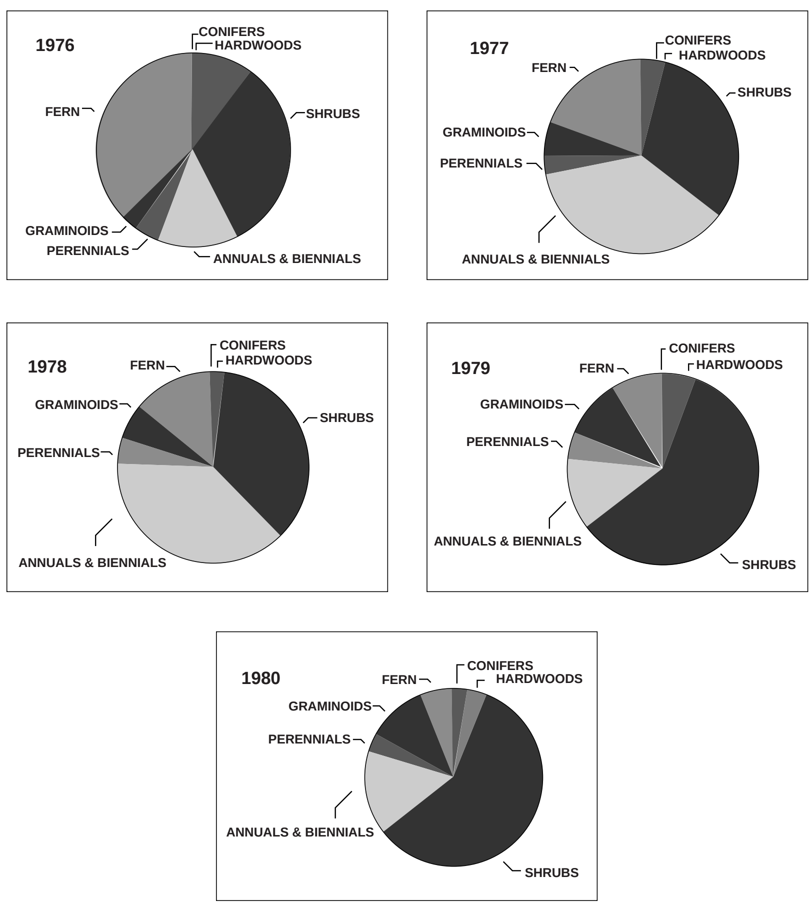


Figure 11—Proportional changes in foliar cover for the various categories of vegetation. Challenge Experimental Forest, 1976-1980.

The categories of vegetation that were poorly represented at the end of the study were the conifers and the perennials. The conifers, which were represented almost entirely by ponderosa pine (*PipoP*), had a frequency value that indicated a clumpy distribution (*table 3*). They also got a late start with none present until 1977 (*table 3*). Thus, they began life with heavy competition in many of the most favorable microsites. Many died. Ponderosa pine seedlings that were alive at the end of the study were those that occupied small areas free of shrubs, clumps of hardwoods, or high densities of annuals and graminoids. The short height of the pines also suggests that some were overtopped and growing slowly. More will die, but those that remain will eventually dominate.

The severe browsing of some shrubs by deer early in the study may actually have aided their development and dominance potential. Deerbrush and whiteleaf manzanita (*Cein3* and *Arvi4*) seemed to have benefited by damage to the main stem, which led to the development of multiple stems at an early age, and increased their potential for higher foliar cover.

The diversity and development of the perennials in this plant community was puzzling. With 21 species present during the study, and a trend of increasing number of species, this category of plants was well represented. However, their contribution to the community in terms of density and cover was relatively small. Not only was their density value at the end of the study only 11 percent of the community and their cover value only 4 percent, but the trend in density was that of a slow increase, and cover was flat. Mean height was actually declining. Perhaps the strategy of the perennials is to first establish a presence, and then await a more suitable environment. Perhaps a condition of being perennial in the environment of this study is to develop better later. Antos and Halpern (1997) found that perennials in a recent clear-cutting in western Oregon had greater root development than annuals, suggesting that this condition probably contributed to their ascendency later in the successional sequence. Previous work on the Challenge Experimental Forest has shown a high proportion of perennials becoming established over a longer timespan in a more shady environment (McDonald and Reynolds 1999).

Although the total number of species increased at the end of the study, this gain was limited to the annuals and perennials. Future increases may be tempered, however, by several factors. The resident species already are numerous and of many categories, plant density is high, and the height of tanoak (*Lide3*) and the shrubs is exploding. Certainly the supply of available resources such as light, nutrients, and water is diminishing. The resident species probably are inhibiting invasion and establishment by preempting available space or more specifically by occupying the habitable microsites. This was readily seen in this study in areas of differing microrelief. Depressions often were occupied by many plants of several species, while nearby mounds were barren. Resident species also modified the environment (more shade for example), which in turn inhibited the germination of seeds and the development of plants that became present.

Sousa (1984) noted that the resources made available by a disturbance are soon exhausted by new colonists and regrowth of survivors. Further growth often is curtailed. At the end of the study, total foliar cover was 17,433 ft^2 per acre or 40 percent. Plainly, space was available for additional horizontal development. But, although increasing, the rate of increase decreased each year from 1977 through 1980. Thus, on a site of high quality, such as this, growth may be more slowed than curtailed, at least during the first 5 years.

Although it is impossible to establish a definitive successional progression in only 5 years, some early trends are noteworthy. Tanoak (*Lide3*) and ponderosa pine (*PipoP*) will be the most abundant trees, and whiteleaf manzanita (*Arvi4*) and deerbrush (*Cein3*) will be the most abundant and dominant shrubs. Tanoak and the shrubs will continue to expand rapidly in foliar cover and height and dominate the plant community for years to come. Ponderosa pine will be scattered in small groups and as single trees. The annuals and graminoids will be increasingly relegated to small openings among the trees and shrubs, and the shade-tolerant perennials likely will increase in numbers and density and reside in both sun and shade environments. Western bracken fern will be present in various amounts almost everywhere.

Consequently, the mode or process of succession is best characterized as "modified" environmental succession. The dominant species of the near future will be those whose regeneration strategies result in early dominance. Sprouting shrubs and hardwoods with burgeoning foliar cover and height are good examples. As the crowns of trees and shrubs close, and the high density of the annuals and graminoids decrease, more shade-tolerant conifers such as Coast Douglas-fir (*PsmeM*) and incense-cedar (*Lide*) and other tolerant perennials and graminoids will become established. Thus, succession will occur through environmental modification. It is not classical replacement of one stage of species by another stage, however, because the first stage will be present for many years. Species of random origin, especially those from windblown seeds, will not be a major part of the understory plant community. Plants from the seedbank in the soil will not be a major part of this community either. However, they will have accomplished their mission because the storehouse in the soil will have been replenished, and they once again will be poised to take advantage of another disturbance.

As ecology becomes more important in forestry, knowledge about plant species and plant communities that develop naturally or after a deliberate manipulation is increasingly needed. Manipulation could be for a variety of reasons: to create a future forest, to provide an economic crop, to grow plants whose seeds or browse would be critical to wildlife, or simply to have present a broad base of species and age classes and thus be able to provide amenities and commodities that will be needed in the future. Data from studies such as this will be invaluable for accomplishing such goals.

References

Antos, Joseph A.; Halpern, Charles B. 1997. **Root system differences among species: implications for early successional changes in forests of western Oregon.** American Midland Naturalist 138: 97-108.

Clements, F.E. 1916. **Plant succession: an analysis of the development of vegetation.** Carnegie Institute Washington Publication 242; 512 p.

Daubenmire, R.F. 1968. **Plant communities: a textbook on plant synecology**. New York: Harper and Row; 300 p.

Dombeck, Mike. 1997. **Concerning criteria for managing healthy forests**. Presented before the subcommittee on forests and forest health, U.S. House of Representatives. March 18, 1997; 13 p.

Egler, F.E. 1954. **Vegetation science concepts: I. Initial floristic composition, a factor in old-field vegetation development.** Vegetatio 4: 412-417.

Gordon, Donald T. 1979. **Successful natural regeneration cutting in California true firs.** Res. Paper PSW-140. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 14 p.

Grime, J.P. 1979. **Plant strategies and vegetation processes**. New York: John Wiley and Sons; 222 p.

Hickman, James C. 1993. **The Jepson manual, higher plants of California**. Berkeley: University of California Press; 1400 p.

Little, Elbert L., Jr. 1979. **Checklist of United States trees (native and naturalized).** Agric. Handb. 541. Washington, DC: Forest Service, U.S. Department of Agriculture; 375 p.

Margalef, R. 1963. **On certain unifying principles in ecology**. American Naturalist 97: 357-374.

McDonald, Philip M.; Fiddler, Gary O.; Meyer, Peter W. 1996. **Vegetation trends in a young conifer plantation after grazing, grubbing, and chemical release.** Res. Paper PSW-RP-228. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 17 p.

McDonald, Philip M.; Lahore, Lona F. 1984. **Lumbering in the Northern Sierra Nevada: Andrew Martin Leach of Challenge Mills.** The Pacific Historian 28(2): 18-31.

McDonald, Philip M.; Reynolds, Phillip E. 1999. **Plant community development after 28 years in small group-selection openings;** 30 p. Manuscript on file at the Pacific Southwest Research Station, Redding, CA.

McDonald, Philip M.; Tappeiner, John C., Jr. 1986. **Weeds: life cycles suggest controls.** Journal of Forestry 84(10): 33-37.

Minore, Don. 1966. **The growth of *Pteridium aquilinum* (L.) Kuhn var. *pubescens* in relation to geographic source, soil nutrients, and forest site.** Corvallis: Oregon State Univ.; 96 p. Ph.D. Dissertation.

Odom, Eugene P. 1969. **The strategy of ecosystem development**. Science 164:262-270.

O'Hara, Kevin L.; Seymour, Robert S.; Tesch, Steven D.; Guldin, James M. 1994. **Silviculture and our changing profession.** Journal of Forestry 92(1): 8-13.

Powers, Robert F.; Oliver, William W. 1978. **Site classification of ponderosa pine stands under stocking control in California.** Res. Paper PSW-128. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 9 p.

Randall, John M. 1990. **Establishment and control of bull thistle (*Cirsium vulgare*) in Yosemite Valley.** In: van Riper, C. III; Stohlgren, T.J.; Veirs, S.D. Jr; Hillyer, S.C., editors. Examples of resource inventory and monitoring in National Parks of California. Proceedings of the 3rd biennial conference on research in California's National Parks; 1988 September 13-15; Davis, CA; 177-193.

Rietveld, W.J. 1992. **Conservation forestry: an idea whose time has come, again**. Tree Planter's Notes 43(3): summer (unpaginated).

Salwasser, Hal. 1992. **An ecosystem perspective for managing the National Forests and Grasslands.** Presented at the Blue Mountains Biodiversity Conference, Walla Walla, WA, 1992, May 29; 16 p.

Smethurst, P.J.; Nambiar, E.K.S. 1990. **Effects of contrasting silvicultural practices on nitrogen supply to young radiata pine.** In: Dyck, W.J.; Mees, C.A., editors. Impact of intensive harvesting on forest site productivity. IEA/BE T6/A6 Rep. 2. Forest Research Institute, Rotorua, New Zealand; 85-96.

Sousa, Wayne P. 1984. **The role of disturbance in natural communities**. Annual Review Ecological Systems 15: 353-391.

Thomas, Jack Ward. 1994. **New directions for the Forest Service**. Statement to members of several committees in the U.S. House of Representatives; 14 p.

U.S. Department of Agriculture. 1994. **Plants of California—alphabetical listing. Report 5.** USDA Soil Conservation Service; 274 p.

U.S. Department of Agriculture. 1997. **Ecological subregions of California, section and subsection descriptions.** Chapter 9. R5-EM-TP-005. San Francisco, CA: Pacific Southwest Region, USDA Forest Service; p 6.

Wagner, Robert G.; Zasada, John C. 1991. **Integrating plant autecology and silvicultural activities to prevent forest vegetation management problems.** The Forest Chronicle 67(5): 506-513.

The Forest Service, U.S. Department of Agriculture, is responsible for Federal leadership in forestry.

It carries out this role through four main activities:

- Protection and management of resources on 191-million acres of National Forest System lands
- Cooperation with State and local governments, forest industries, and private landowners to help protect and manage non-Federal forest and associated range and watershed lands
- Participation with other agencies in human resource and community assistance programs to improve living conditions in rural areas
- Research on all aspects of forestry, rangeland management, and forest resources utilization.

The Pacific Southwest Research Station

- Represents the research branch of the Forest Service in California, Hawaii, American Samoa, and the western Pacific.

United States
Department
of Agriculture

Forest Service

**Pacific Southwest
Research Station**

Research Paper
PSW-RP-239

Diversity, Density, and Development of Early Vegetation in a Small Clear-cut Environment