

A PRACTICAL APPLICATION OF DISCRIMINANT FUNCTIONS FOR CLASSIFYING
SUCCESSIONAL VEGETATION COMMUNITIES IN THE FIRST TEN YEARS
FOLLOWING LOGGING OF COAST REDWOOD FORESTS, IN REDWOOD NATIONAL PARK

William S. Lennox, Esteban H. Muldavin, James M. Lenihan,
and Stephen D. Veirs, Jr.

Abstract. Successional patterns in one to ten-year old vegetation established following logging of upland redwood forest have been determined for the lower Redwood Creek basin in north-western California. A classification of successional vegetation types was developed using cluster analysis and tabular comparison of releves. Two main groups were identified. The first included four remnant vegetation types re-established where disturbance due to logging was low. Where logging resulted in severe soil disturbance or removal, a more weedy flora became established which was divided into six types through a moisture gradient. Multiple discriminant analysis models were derived for the classification and can be used to predict potential vegetation on sites poorly revegetated or newly denuded in the watershed rehabilitation process in Redwood National Park.

INTRODUCTION

Redwood National Park was expanded in 1978 by 48,000 acres including approximately 36,000 acres of cutover forest lands which had previously been dominated by stands of coast redwood (Sequoia sempervirens) and Douglas-fir (Pseudotsuga menziesii). With expansion, an extensive watershed rehabilitation program was authorized to control erosion and sedimentation and to reduce risk of damage to streamside areas on Redwood Creek. Part of this rehabilitation program (USDI, 1981) includes the use of plants for erosion control and to re-establish the natural vegetation of the parklands. This study was designed to investigate the patterns of vegetation succession on the recently logged forest lands as an aid in determining correct plant species or use on freshly denuded rehabilitation sites and inadequately revegetated areas of the park.

Previous research describes succession following logging in redwood as a rapid transition from a period of dominance by short-lived weeds followed by hardwood brush invasion and then conifer dominance. This is influenced by the proximity of seed source, slash treatment and soil surface conditions (Pritz, 1959). In the first five years after logging, herbaceous vegetation is most abundant. In the second five years, herb cover decreases and becomes quite scarce after ten years have passed. Shrubs are not abundant until six to ten years and remain dominant for an 11 to 20 year period. After 20 to 30

National Park Service, Redwood National Park, Arcata, California 95521

years, conifers become the dominant cover (Dassman, 1968; Zinke, 1977). Waring and Major (1964) indicate that, in general, after disturbance by cutting or fire, light demanding species assume dominance, but the majority of original forest species are still present.

In this study, we describe in greater detail the pattern of early succession that occurs prior to re-establishment of conifer dominance and explore some of the underlying environmental conditions that may determine this pattern. This is done by constructing a classification (using cluster analysis and tabular comparison) of the vegetation communities that incorporates the successional processes as part of the community descriptions. Statistical models are then derived (using multiple discriminant analysis) to evaluate the factors which influence community development. These models may be used as a management tool for vegetation mapping, for direct site evaluation and for species selection for planting as part of the rehabilitation program for Redwood National Park.

STUDY AREA

The study area is in Redwood National Park within the Redwood Creek watershed of north coastal California. The Redwood Creek watershed trends in a north-northwest direction for 55 miles between adjacent drainages of the Mad and Klamath rivers; however, only the lower quarter of the watershed is included in the study area. This area consists of approximately 50,000 acres (20,250 ha) of which 36,000 acres (14,200 ha) are logged, 12,000 acres (4,850 ha) are virgin redwood forest, and 3,000 acres (1,200 ha) are coastal prairie.

The upland virgin forest vegetation of the study area can be described from preliminary results of vegetation classification studies by Lenihan (1981) in the undisturbed Little Lost Man watershed adjacent to the study area. These results suggest that the natural upland redwood vegetation of the lower Redwood Creek basin can be classified into three distinct types. The moist type is generally found at lower elevations, especially on lower, concave slopes. The mesic type is generally found at mid-elevations, especially on even topography. The dry type is generally found at higher elevations, especially on convex ridges.

Redwood Creek flows through the center of the study area, following the trace of the Grogan Fault. The basin's west side is underlain by the Kerr Ranch Schist, and dominated by the Masterson soil series. In contrast the east side is underlain by the Franciscan formation and dominated by the Hugo soil series.

The climate is maritime-mediterranean with rainfall occurring primarily from November through March. The summer months are characterized by coastal fog that may extend 15 miles or more up the basin.

The study area was subjected to intensive logging in the mid-1950's and continuing until park expansion in March, 1978. Early logging left scattered overstory seed trees. Clearcutting was the main logging method in the 1960's and 1970's using either tractor or high lead cable yarding. Tractor yarding was the most common, particularly on the older, higher elevation sites. Cable yarding did not become common until the lower slopes adjacent to the old boundaries of the park were reached. Only two units were cable yarded prior to 1973.

Slash burn following logging was a widespread practice but was not uniform. The majority of tractor yarded sites were burned whereas the majority of cable sites were not. Some sites were burned more than once with extensive hot fires, eliminating most logging debris and killing the residual vegetation. On other sites, burning was spotty and light, eliminating some litter and light slash, but leaving large areas of vegetation.

The variability in pre-logging vegetation, logging practice and environmental factors including aspect, elevation, and parent material has resulted in a complex mosaic of post-logging vegetation communities in the Redwood Creek drainage.

SAMPLING METHODS

A long-term study of successional change on a site was impractical because of the time limitations and immediate management needs. Instead, a sampling strategy of site-to-site comparisons was adopted. Many sites, in differing stages of development were compared and the successional processes inferred by grouping sites of similar floristic composition and environmental conditions into an age sequence. This then becomes a problem of analyzing vegetation patterns made complex by rapid successional processes. Our approach was to develop a classification of successional vegetation types to define the vegetation pattern. From the classification we analyzed the relationships of change in vegetation composition and structure within a particular vegetation type and relationships of vegetation types among each other, independent of time, as to their differing floristic and environmental characteristics.

Preliminary vegetation types were defined by a field reconnaissance in which the general species combinations that occur were identified. Each combination was then sampled by establishment of a "releve" or a plot within a floristically homogenous area (Mueller-Dumbois, 1974). Minimal plot size for the releve was established by developing species area curves from nested test plots. The minimal area was found to be 35 m² (400 ft.²). Our relevés ranged from 35 - 110 m², averaging 80 m².

Each releve included a complete inventory of vascular species stratified by height class: herbs (<1 m), shrubs 1 - 5 m), and trees (>5 m). Each species in each strata was assigned a cover-degree abundance value according to the Braun-Blanquet scale (Becking, 1957).

The following variables were also recorded: (1) Aspect with a hand compass; (2) Elevation from U.S. Geological Survey topographic map; (3) Slope in percent using a clinometer; (4) Terrain/Treatment factors: a. Tractor skid trails resulting from tractor yarding at harvest, b. Relatively undisturbed areas between tractor skid trails or "tractor islands," c. Evidence of cable yarding at harvest, d. Seepage areas or wet slumps, e. Sidecast or cutbanks of roads, f. Haul roads or landings, (5) Slope position calculated as the ratio (in percent) of the distance of a releve to the nearest drainage over total distance from ridgetop to drainage; (6) Percent slash cover by visual estimate; (7) Slash burning evidence present or absent; (8) Soil parent material; (9) Percent exposed mineral soil, or the percent of A Horizon soil removed, by visual estimate; (10) In addition, a soil profile on selected relevés was taken with a hand auger with information recorded on soil horizons, color, depth, texture, structure, percent clay, rooting type and depth;

(11) The time since harvest of a site was determined from harvest records, historical aerial photographs or from annual ring counts on sprouting redwood. No complete harvest record was available at the onset of the project, thus sites were initially classified into broad age classes: young, medium, and old, until a definite timber harvest data could be assigned. This resulted in unequal size samples per year class in the final analysis.

A total of 361 releves were taken from June through September, 1979. Only sites logged between 1970 - 1978 were sampled (no logging occurred after March 1978). This represents an age span of one to ten years between logging and sampling.

DATA TRANSFORMATION AND ANALYSIS

The analysis was divided into three phrases: (1) The data transformation for analysis and computer processing; (2) The development of a hierarchical classification of successional vegetation types based on floristic composition using cluster analysis and tabular comparison techniques; (3) The development of multiple discriminant analysis statistical models (MDA) to quantitatively define the vegetation types floristically and environmentally. Finally optimal MDA models using a step-wise procedure for practical application in watershed rehabilitation and vegetation mapping were developed.

The releves were stratified into five age classes based on date of timber harvest: 1970 - 1972, 1973 - 1974, 1975, 1976, 1977 - 1978. The 1977 and 1978 sites were aggregated because the 1978 sites were harvested in early spring before the growing season and thus were more closely aligned with those of the previous season. Because changes in vegetation composition and structure appeared to occur at a slower rate with increasing age, the older sites were also aggregated to simplify the analysis.

The cover/abundance degree scale used in the field to record species cover was transformed to facilitate computer processing and numerical analysis after a scheme developed by Marrel (1979). The azimuth readings were transformed into a "solar exposure index" modified from Sawyer's Site Moisture Equivalency Index (1971). Azimuths are scaled from 1 to 16, with 1 being the warmest and 16 the coolest.

Since a species could be recorded in three different height strata, three independent records could result for the same species. We call each record a "species property." This study contains more than 250 such species properties based on observations of 180 different species in one or more height strata.

The classification phase of the analysis was an iterative process combining cluster analysis and classical phytosociological tabular comparison techniques to develop a hierarchical classification of successional vegetation types based on floristic composition.

Cluster analysis is essentially a tool for organizing data by associating similar entities (releves) into classes. The approach used was polythetic and agglomerative as described by Orloci (1967).

Due to both computer limitations and the need to reduce the dimensionality of the study, a maximum of 100 species properties were actually used in the numerical analysis at one time. The criterion for selection of a species

property was its presence in more than 5% of the total sample of releves, or 5% constancy, as defined by Becking (1957). Each age class was clustered separately using the same set of 100 species properties and their transformed cover values.

The cluster analysis was interpreted using tabular comparison. Synthesis tables (Becking, 1957) were constructed with releves in their clustered order in columns and species in rows. In this form, releve and species relationships can be directly analyzed by inspection. The determination of "significant" clusters is a matter of ecological interpretation based on acceptable levels of within group heterogeneity (based on cluster within group dispersion) and the location of differential species on the tables. Differential species are those species which serve to separate or define clusters on the basis of either their restriction to, or their high cover in, certain clusters. Significant clusters generally fell between 25% and 75% average within group dispersion. Above the 75% level, clusters tended to be highly heterogeneous. Either they could be separated at lower levels of the hierarchy into clusters clearly defined by differential species or they contained single anomalous releves that were clusters unto themselves because they were either unique or too heterogeneous in composition to classify at a lower level. These releves were labeled as transitional and not used in further group analysis.

Through an iterative process of rearranging releve and species orders on tables, blocks of differential species and associated releves were delineated, which defined types within each age class. We then grouped similar clusters, based on differential species blocks, from each age class and constructed the final classification of successional vegetation types. This classification describes the major vegetation communities and their successional progression from one to ten years after logging. This process is a modified version of the tabular comparison techniques outlined by Becking (1957) and Mueller-Dombois and Ellenberg (1974).

The next phase was to develop statistical models using multiple discriminant analysis to quantitatively define the floristic classification arrived at through cluster analysis and tabular analysis comparison, and to examine some of the possible extrinsic environmental factors which influence the successional patterns.

There are two objectives in the practical application of the vegetation type classification and associated MDA models. First, where vegetation is present, to classify and map it using MDA models based on floristic and environmental criteria together. Second, if vegetation is absent, as in the case after earth moving in rehabilitation of a site, to be able to predict potential vegetation using MDA models based solely on environmental criteria.

VEGETATION TYPE CLASSIFICATION & DESCRIPTION

The vegetation types are classified into two broad groups, Remnant and Invasion, based on the nature of species establishment. The Remnant Group is characterized by species common in the virgin forest understory which survived timber harvest and flourished. The typical dominant species are Rhododendron macrophyllum, Lithocarpus densiflora, Vaccinium ovatum, Gaultheria shallon, and Polystichum munitum. Other species such as Oxalis oregona, Blechnum

spicanth, and Vaccinium parvifolium may be present but generally are not dominant. A sparse, scattered tree overstory may also remain, consisting of Tsuga heterophylla or Arbutus menziesii and occasionally Sequoia sempervirens and Pseudotsuga menziesii.

Within the Remnant Group, the vegetation types are described as follows:

1. Polystichum munitum/Oxalis oregana Type (P/O)
This type is dominated by Polystichum in both the herb and shrub layers. Oxalis, Blechnum spicanth and Galium triflorum are characteristic components of the herb layer. Generally all remnant species begin with some cover and gradually increase until the site is covered. Gaultheria shallon, though it does not reach its optimum in this type, can be important in later years, co-dominating with Polystichum. Invading species such as Erechtities prenanthoides can be strong early, but fade after the third or fourth year.
- 2a. Rhododendron macrophyllum/Vaccinium ovatum Type (R/V)
This type is characterized by the dominance of Rhododendron, V. ovatum, and Lithocarpus in both the herb and shrub layers. In this type, total Rhododendron cover stabilizes by year three. Gaultheria, though present, develops little cover until year five after a decline of Rhododendron as it develops from a multi-branched sprouting form to a giant shrub. Loss of lower leaves effectively increases habitat available at ground level for Gaultheria.
- b. Rhododendron macrophyllum/Gaultheria shallon Subtype (R/G)
This subtype, like the R/V typic type, is dominated by Rhododendron, Vaccinium ovatum and Lithocarpus in the shrub layer, but by Gaultheria in the herb layer. Rhododendron fails to develop significant cover as a multi-branched sprouter allowing Gaultheria to dominate. Gaultheria is initially on the sites with fairly high cover (35%) and increases until year four with Rhododendron following a similar pattern in the shrub layer as a few branched giant shrub.
3. Lithocarpus densiflora/Whipplea modesta Type (L/W)
This type is dominated by Lithocarpus in the tree and shrub layers, with Pseudotsuga menziesii occasionally co-dominating. Whipplea forms a low-lying mat under sprouting Lithocarpus. Lithocarpus definitely reaches its optimum in this type, but this vegetation type was found only in the older age classes (year five through nine), and the early phase remains undefined.

In contrast to the Remnant Group, the Invasion Group is characterized by species that are rare or absent in the virgin forest and invade the site after timber harvest. Examples are Alnus oregana, Ceanothus thyrisflorus, Baccharis pilularis, Carex dewyana, and Equisetum telmateia. The early years are often dominated by short-lived weedy species, including exotics such as Erechtities prenanthoides, E. arguta, Anaphalis margaritacea, Ganaphalium chilense, G. purpureum, G. californicum and Epilobium paniculatum. Remnant type species may be present, but usually they have low cover values and are often merely maintaining themselves on the site or declining. There are exceptions such as Iris douglasii, Arbutus menziesii, and Whipplea modesta which are capable of establishing themselves on new substrates and flourish with invading species.

The Invasion Group vegetation types are as follows:

1. Ceanothus thrysiflorus/Arbutus menziesii Type (C/A)

This type is almost exclusively dominated by Ceanothus with Arbutus, particularly in the shrub layer of older sites. Ceanothus attains an average cover of 70% by year eight and still has not peaked. At year three, when Ceanothus shrub cover peaks and it enters the tree layer, most other species are on the decline except for Arbutus which steadily increases in cover. Baccharis initially has a strong growth rate in competition with Ceanothus, but Ceanothus eventually prevails. Whipplea has a moderate cover in the younger years but also declines as the Ceanothus canopy increases. Smaller Ceanothus individuals decline in number as the dominant canopy closes. Ceanothus occurs primarily as a single age class.

2a. Baccharis pilularis/Whipplea modesta Type (B/W)

This is the most prevalent type within the study area. Both Baccharis and Whipplea attain their greatest cover in this type, dominating in the shrub and herb layers respectively. Both species increase in cover rapidly in the first three to four years and peak at five to six years. Unlike Ceanothus in the C/A type, Baccharis maintains reproduction, to some degree, after shrub layer establishment. Remnant type species can be present but generally do not flourish except for Iris and Whipplea.

b. Pseudotsuga menziesii/Whipplea modesta Subtype (P/W)

This subtype is also similar to the B/W typic type except that Pseudotsuga replaces Baccharis as the dominant in the shrub layer. This type is found only in older age classes and may reflect the silvicultural treatment (aerial seeding) during that time period.

c. Hypochoeris radicata/Aira caryophylla Subtype (H/A)

This subtype is also similar to the B/W type except that Baccharis, though present, is not robust and fails to reach shrub height (1 m), even after nine years. Overall vegetative cover is lower than cover for other types. Hypochoeris, Aira, and Lolium spp. replace Whipplea as the dominant ground cover.

3. Alnus oregona Type (A/A)

This type is dominated in all layers by Alnus. Whipplea can be an important component in the herb layer in early years; but after crown closure of Alnus, it declines. Baccharis pilularis shows a similar trend, increasing early and then declining when outpaced by Alnus.

4. Juncus effusus/Equisetum telmateia Type (J/E)

This is a broadly defined type which is characterized by dominance or co-dominance of several wet-site species including Juncus effusus, J. Bolanderi, J. Bufonius, Carex dewyana, Petasites palmatus, Typha latifolia, and E. telmateia, or E. arvense. Cover for any combination of species appears to reach a peak at year three and is maintained at a more or less constant level the remaining six years with little evidence of successional progression to a shrub community of either Baccharis or Alnus dominance.

STATISTICAL MODELS OF THE VEGETATION TYPE CLASSIFICATION

For each level of the classification hierarchy, separate floristic and environmental Multiple Discriminant Analysis (MDA) models are derived, beginning with the Remnant and Invasion groups. An MDA was used to separate the groups based on floristic dissimilarities using 40 species that showed differential character in the constancy table. A total of 306 relevés were used: 206 from the Invasion Group and 100 from the Remnant Group. A single discriminant function was generated which had a highly significant Chi-square ($P < .001$).

THE REMNANT GROUP VEGETATION TYPE

An MDA was generated to quantitatively model the floristic difference among the Remnant Group vegetation types only. It was based on the 100 relevés used to represent the Remnant Group in the previous MDA. Though the R/G Type is considered a subtype in the classification, for simplicity in analysis, it was entered in the MDA models at the same level as the other types. Twenty-three differential species were used as variables and the maximum of three significant discriminant functions were derived. The relative classification efficiency was 98% correct reclassifications indicating that the model, at least internally, is effective in differentiating vegetation types floristically.

To test for significant environmental characteristics that might be correlated with the floristic expression, another MDA was generated based on 11 environmental variables. Of the possible three functions, only the first two were significant and used in further analysis. These two functions together accounted for 97.5% of the total variation.

INVASION GROUP VEGETATION TYPES

A floristic MDA model of the Invasion Group vegetation types was generated on the basis of 30 species and 206 relevés of the Invasion Group divided into their respective types. As with the Remnant model, the subtypes of the Baccharis/Whipplea (B/W) type have been considered at the same level as the types to simplify the analysis. The maximum of five significant functions were derived with a very high discriminatory power of 99.9% of the variation in the discriminant space attributed to group differences. The relative classification efficiency was 92% indicating that the Invasion Group vegetation types are also well differentiated floristically.

To determine if there are also significant environmental differences between the types, a MDA was generated based on the same relevés and 15 environmental variables. Of five discriminant functions possible, the first four were significant ($P < .01$), accounting for 98.9% of the total variation.

APPLICATION OF MODELS, THE OPTIMAL MODEL

For practical application in evaluation of existing or potential vegetation for sites being rehabilitated within Redwood National Park, "optimal" or easily applied MDA models were developed. These models were constructed by selecting variables that were easily measured in the field and then applying a stepwise MDA procedure to determine the best discriminators. This selection process

resulting in reduced dimensionality (fewer variables) in the optimal models, but enough variables were retained to maintain the relative classification efficiency above 90% for the combined floristic/environmental models and 75% for the environmental models. The procedure for site evaluation and mapping using the optimal models is described in a separate paper (Lenihan, et al., 1981). It includes a field procedure, a vegetation type key derived from the optimal model and applications of new sites using the program to compute vegetation types from floristic/environmental data or environmental data only (for denuded sites) is also provided.

DISCUSSIONS AND CONCLUSIONS

From the classification and associated MDA models we can recognize two gradients of disturbance and moisture that affect succession after timber harvest in upland redwood forest vegetation. The influence of disturbance separates the Remnant Group of vegetation types from the Invasion Group. This is primarily a function of terrain (logging treatment) factors, which are correlated to present mineral soil exposure, slash accumulation and slope. The sites may range from the slightly disturbed tractor island, with an intact surface soil, through the cable yarded condition with moderate disruption of the skid trail which may have little or none of the original soil moisture remaining. Logging also disrupts normal drainage patterns and soil moisture conditions. Examples include the re-direction of subsurface flows of surface water along skid trail patterns resulting in the dewatering of steep slopes and lowering of soil moisture levels. Conversely, the impoundment of water in areas of limited drainage and low slope may also result from logging caused changes in local topography. Overlain on this distribution a factor is an overall moisture gradient as measured here by separate individual vegetation types within the main groups. The hydric to xeric conditions occur on cool northern aspects, at low elevation or low slope position and near the mouth of the basin. In contrast, the xeric conditions are found on the warmest southern exposures, high elevations or slope position and inland away from the influence of the ocean.

In the low disturbance conditions among the Remnant Group, the Polystichum/Oxalis (P/O) type occupies the moist end of the gradient; the Rhododendron/Gaultheria (R/G) type, the moist mesic; the Rhododendron/Vaccinium (R/V) type, the mesic and the Lithocarpus/Whipplea (L/W) type, the dry mesic. A remnant type of the xeric condition is undefined. Additional field work may have resulted in definition of this type; however, the widespread impact of slash burning on these sites appears to have pushed the post logging vegetation into the Ceanothus/Arbutus disturbance type.

The Remnant Group successional vegetation types, as a whole, correspond closely to the herb and shrub unions described by Lenihan (1981) for upland virgin redwood forest types. Analogous remnant types are found following logging in the Pseudotsuga/Tsuga forest of the western Cascades of Oregon. Polystichum, Rhododendron, and Gaultheria are particularly important as shrubs in early succession (Steen, 1966; Morris, 1958; Issac, 1940). Dyrness (1973) has shown that on undisturbed soils Polystichum and Oxalis may dominate moist sites and Rhododendron, Vaccinium parvifolium, and Gaultheria on drier sites. Similarly, Yerkes (1960) mentions Oxalis showing preference

for north-facing slopes and Whipplea south-facing. In the redwood region Zinke (1977) indicated that Polystichum can be common in the pioneer sere of his Redwood-Grand Fir forest type and that Whipplea is important in his Redwood-Douglas-fir hardwood type in conjunction with Lithocarpus and Arbutus.

As disturbance increases, the Invasion Group revegetation types become dominant. The Juncus/Equisetum and Alnus types occupy the hydric and moist mesic conditions respectively. Alnus is a common successional type in the Cascades supplanting Polystichum and associates with increased disturbance on moist sites (Franklin, 1979). In the redwood region, Becking (1966) mentions Alnus as a common successional species following natural disturbance in his Redwood/Oxalis alliance.

As conditions become more mesic the Alnus type gives way to the Hypochoeris/Aira type on highly disturbed sites and the Pseudotsuga/Whipplea and Baccharis/Whipplea types on less disturbed sites. The Baccharis/Whipplea type has elements of the North Coastal Shrub as described by Heady, et al., (1977) and Munz and Keck (1959) except instead of Gaultheria and Polystichum, Whipplea is the dominant herb (though the others can be present). The Pseudotsuga/Whipplea type results under similar conditions where aerial seeding was successful after harvest.

On the dry mesic to xeric sites that have been burned the Ceanothus/Arbutus type predominates. Zinke (1977) and Waring and Major (1964) indicate that normal succession in redwood can be shunted to Ceanothus chaparral similar to that described by Hanes (1977) except for the influence of Arbutus which is an element of the Mixed Evergreen Forest (Sawyer and Thornburg, 1977). Ceanothus thyrsiflorus chaparral is reported to extend into southwestern Oregon, primarily on burned sites (Hanes, 1977; Ingram, 1931).

In general the pattern of succession after timber harvest follows this trend: in the first three years short-lived annual and biannual herbs dominate followed by the development of shrub communities either from remnant plants that have survived timber harvest and flourished or from invading species capitalizing on the disturbed environment. The exceptions are the hypochoeris/Aira and Juncus/Equisetum types, which occupy the most disturbed, driest and wettest types respectively. These show little trend towards shrub community development over 10 years time. It is probable that these sites will remain little changed as the second growth forests develop around them. Eventually reduced light levels eliminate all but the most shade tolerant species.

Successional patterns occurring on cutover redwood forest land beyond the period investigated in this paper remains to be examined in detail. Preliminary observations suggest that tree canopy closure can occur in ten to twenty years, depending on tree density. Harsh disturbed sites are slowest. Smaller areas of the Hypochoeris/Aira subtype remain unforested until tree canopies close over them from adjacent vegetation. Ceanothus/Arbutus stands may persist for twenty or thirty years, suppressing conifer growth until senescence breaks up the Ceanothus canopy. Repeated burning would be expected to perpetuate the Ceanothus/Arbutus type. In the absence of extensive burning, Pseudotsuga, Lithocarpus, and Arbutus dominated stands with Sequoia

are expected to develop. In many cases, the trees which may eventually dominate these Ceanothus/Arbutus sites were established at the same time as the Ceanothus, but survive in a suppressed condition until the Ceanothus becomes senescent.

On most sites closure of a canopy dominated by Pseudotsuga and lesser numbers of Sequoia is expected followed by a rapid decline in cover for understory species. As these stands mature and competition related mortality opens the canopy slightly, shade tolerant native species are expected to recover their predisturbance dominance. On Alnus sites, Alnus outstrips other tree species in height growth, rapidly forming a canopy which may remain intact fifty or more years. As the Alnus reaches senescence, Sequoia, Picea, Tsuga, and a few Pseudotsuga established at the same time as the Alnus will escape suppression and form the dominant long term forest canopy. Eventually Alnus is relegated to occasional openings resulting from natural disturbance factors.

With the exception of the Juncus/Equisetum type future tree dominants are usually present as seedlings in each of these early succession vegetation types. The duration of the successional pathway leading to reestablishment of forest conditions similar to the pre-logging pattern may be protracted. Pseudotsuga for example is strongly overrepresented in the post logging forests. Since this species may live well over 500 years in the study area (Veirs, 1981) the return to natural tree densities for the various types will take centuries.

Natural patterns of secondary succession in redwood forest revegetation are undescribed. Continuing studies in the forests of Redwood National Park and its surroundings are expected to bring about an understanding of the natural successional dynamics of virgin redwood forest vegetation, the alterations resulting from modern human activity and the measures which may be necessary to perpetuate these forests as a naturally functioning vegetative system.

LITERATURE CITED

- Becking, R. W. 1957. The Zurich-Montpellier School of Phytosociology. *Botan. Rev.* 23:411-488.
- _____. 1966. The ecology of the coastal redwood forest and the impact of the 1964 floods on redwood vegetation. Final Report, Nat. Sci. Foun. Grant #3468.
- Dassman, F. R. and W. W. Hines. 1958. Logging, plant succession, and black-tailed deer in the redwood region. Mimeograph. Humboldt State University. 12 pp.
- Dyrness, C. T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. *Ecology.* 54:57-69.
- Fritz, E. 1959. Characteristics, utilization, and management of second growth redwood. Foun. for Amer. Res. Mgt., San Francisco, California. 34 pp.

- Franklin, J. F. 1979. Vegetation of the Douglas-fir region. Reprint from: Forest Soils of the Douglas-fir Region. Washington State University Co-op Ext., Pullman, Washington. pp. 93-112.
- Went, T. L. 1977. California chaparral. Chapter 12 in: J. Major; M. G. Barbour (eds.). Terrestrial Vegetation of California. J. Wiley, New York. 1002 pp.
- Went, H. F., T. C. Foin, M. M. Hektner, D. W. Taylor, M. G. Barbour, and W. J. Barry. 1977. Coastal prairie and northern coastal scrub. Chapter in: J. Major and M. G. Barbour (eds.). Terrestrial vegetation of California. Wiley-Sons. New York. 1002 pp.
- Wright, D. C. 1931. Vegetative changes and grazing use on Douglas-fir cut-over lands. Jour. of Agric. Res. 43:387-417.
- Wright, L. A. 1940. Vegetative succession following logging the Douglas-fir region with special reference to fire. Jour. For. 38:716-721.
- Wright, J. M., W. S. Lennox, E. H. Muldavin, S. D. Veirs, Jr. 1981. Guidelines for classifying early post logging vegetation in the lower Redwood Creek basin. National Park Service. Redwood National Park. Technical Report No. 7.
- Wright, E. van der. 1979. Transformation of cover-abundance values in phytosociology and its effect on community similarity. Vegetatio. 39:97-114.
- Wright, W. G. 1958. Influence of slash burning on regeneration, other plant cover, and fire hazard in the Douglas-fir region (a progress report) USDA Forest Service Pacific Northwest Forest and Range Exp. Sta. Res. Pap. 29. 49 pp.
- Wright-Dombois D. and H. Ellenburg. 1974. Aims and methods of vegetation ecology. J. Wiley and Sons, New York. 547 pp.
- Wright, P. A. and D. D. Keck. 1973. A California flora with supplement. University California Press. Berkeley, California. 1681 and 244 pp.
- Wright, L. 1967. An agglomerative method for classification of plant communities. Jour. of Ecol. 65:193-206.
- Wright, J. O. and D. A. Thornburg. 1971. Vegetation types on granodiorite in the Klamath mountains, California. Report to Pac. S. W. For. and Ran. Exp. Sta.
- Wright, J. O. 1977. Mixed evergreen forest. Chapter 10 in: J. Major and M. G. Barbour (eds.). Terrestrial vegetation of California. J. Wiley and Sons, New York. 1002 pp.

- Steen, H. K. 1966. Vegetation following slash fires in one western Oregon locality. Northwest Sci. 40:113-120.
- U. S. Department of the Interior, National Park Service. 1981. Watershed Rehabilitation Plan. Denver Service Center. Denver, Colorado.
- Veirs, Stephen D., Jr. 1981. The influence of fire in coast redwood forests. In: Proceedings of the fire history workshop (Oct. 20-24, 1980. Tucson, Arizona). U. S. Department of Agriculture, For. Serv. Gen. Tech. Report. RM81, Rocky Mt. For. and Ran. Exp. Sta. pp. 93-95.
- Waring, R. H. and J. Major. 1964. Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light, and temperature. Eco. Mono. 34:167-215.
- Yerkes, V. P. 1960. Occurrence of shrubs and herbaceous vegetation after clear cutting old-growth Douglas-fir in the Oregon Cascades. USDA Forest Serv. Pac. Northwest For. and Ran. Exp. Stat. Res. Pap. 34. 12 pp.
- Zinke, P. J. 1977. Redwood forest and associated north coast forest. Chapter 19 in: Terrestrial vegetation of California. J. Wiley and Sons. New York, New York. 1002 pp.