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A Conceptual Model to Characterize Internal Structure of Plant Communities Based on Functional Traits in Camp Williams, Utah, and Camp Grayling, Michigan

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A CONCEPTUAL MODEL TO CHARACTERIZE INTERNAL STRUCTURE OF PLANT COMMUNITIES BASED ON FUNCTIONAL TRAITS IN CAMP WILLIAMS, UTAH, AND CAMP GRAYLING, MICHIGAN

by

Patricia Hernandez de la Rosa

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR IN PHILOSOPHY

in

Ecology
(Forest Resources)

UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

A Conceptual Model to Characterize Internal Structure of Plant Communities Based on Functional Traits in Camp Williams, Utah, and Camp Grayling, Michigan

by

Patricia Hernandez de la Rosa, Doctor of Philosophy

Utah State University, 2002

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Department: Forest Resources

How plants from a common species pool form community has been considered from a variety of approaches. A promising approach involves the search for assembly rules based on plant functional traits. This approach has potential to provide insight into community and ecosystem processes.

In this research, a general and simple conceptual model based on life forms and independent of species is used as a framework for assessing the internal structure of plant communities. Plant functional traits are used to identify patterns within and between plant communities in the contrasting environments of Camp Williams, Utah, and Camp Grayling, Michigan.

The conceptual model has three different functional types formed by one to three functional groups. A functional group, made up of species with similar life form, is analogous to a vegetation stratum. A functional type, consisting of one or more functional groups, is analogous to a community or vegetation type.

Correspondence analysis (CA) and analysis of variance (ANOVA) indicate that richness, species diversity, and trait diversity are essentially independent of functional type and are, for example, fairly consistent regardless of climatic regime or structural complexity. Cover, on the other hand, increases with the number of functional groups in a functional type.

Consistent patterns and trends for sets of functional traits support the view that assembly rules may account for internal structure in plant communities. The consistent association of sets of traits with functional groups even in taxonomically dissimilar communities suggests that the functional traits are related to fundamental ecological processes that shape these communities.

Ambiguity in some of the results might be explained by extending the analysis to additional installations that replicate the climatic conditions found at Camp Williams and Camp Grayling.

(120 pages)

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Patricia Hernandez-de la Rosa

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CHAPTER 1

INTRODUCTION

Ecologists have been trying to develop a theoretical framework to understand, explain and predict the reality of vegetation change and heterogeneity since ecology was first recognized as a discipline (Diaz et al. 1998). Development of this theoretical framework is through a system of concepts, laws and empirically-based generalizations (Glenn-Lewin et al. 1992).

Beyond interest in the theoretical framework for observed patterns in vegetation, there are practical reasons for predicting vegetation dynamics. Examples include forest and range production and the consequences of management decisions, as well as the preservation of plant and animal species, biotic communities and productive and aesthetically pleasing landscapes. All of these require a thorough knowledge of the patterns and processes of vegetation change. On a global basis, one of the advantages to detecting general rules for observed patterns in plant community structure is the increased need to make predictions under different scenarios. Growing concern about climate change requires predictions of vegetation change at different spatial and temporal scales (Glenn-Lewin et al. 1992).

There is a need to understand the ways that vegetation manipulation, for a variety of management objectives, will affect a broad range of ecosystem functions and processes. Even the "passive management" of historical disturbances regimes considered by Long & Heister (1998) affects ecosystem attributes at both stand and landscape levels.

Plant communities are complex, particularly with respect to the mechanisms and processes that allow establishment, development, persistence and evolution of species. One of the focuses in community ecology has been the study of regularity in nature and the processes than generate it (Drake 1990; Gitay & Wilson 1995). Community structure develops through interactions among species in space and time, operating against a background of environmental variability and chance events.

Assembly rules are one of the approaches taken to identify and understand repeated patterns in plant communities (Drake 1990; Weiher et al. 1998). Assembly rules are generalized restrictions to species coexistence that determine which components of a species pool will form a community.

Plant functional types and plant functional traits are tools used to identify regularity in plant community associations, and they are mostly based on function. Functional traits are important ecological frameworks for describing biological traits, mechanisms and processes underlying vegetation response in ecosystems.

This study presents a conceptual model based on life forms that will allow the description of the internal structure within and between plant communities based on a set of functional traits. Detailed description of the internal structure in communities is undertaken to address some general questions: (1) are there a sets of traits that can be used to characterize a plant community? (2) are there similar sets of traits that can be identified consistently in taxonomically different communities? (3) are there sets of traits that define functional groups within a community, and are those groups similar when compared between similar functional groups in different community types? (4) are there trends or patterns in traits within and between communities?

CHAPTER 2

THE STUDY OF PLANT COMMUNITY STRUCTURE: AN HISTORICAL PERSPECTIVE

The first generation of plant community ecologists devoted considerable attention to the distribution, composition and classification of plant communities; they were particularly concerned with why certain structures appeared to be associated with soils and climate (Crawley 1986; Barnes et al. 1998). Examples of this pioneering work, including Humboldt (1806), Schimper (1898), Gradmann (1898), and Warming (1909), are reviewed by Barnes et al. (1998). Further development in plant ecology has focused on questions relating to species richness, species abundance and patterns of spatial and temporal change.

During much of the last century, ecologists have struggled with the nature of plant communities. Fundamental ideas about how communities are structured were developed by Tansley, Ellenberg and Whittaker, among others (Keddy & Weiher 1999). However, two of the most influential contributions by pioneering community ecologists were the "deterministic view" of F. E. Clements with the idea that communities are discrete association of species and the "individualistic view" of H. A. Gleason that communities are random associations of species simply able to tolerate local environmental conditions. These contrasting views of plant community structure have had remarkable influence on community ecology, and there is still not any clear consensus about which view is more generally applicable. Researchers continue to revisit the ideas of Clements and Gleason to formulate and support hypotheses with varied objectives (Weiher & Keddy 1999;

Booth & Larson 1999; Keddy & Weiher 1999; Wilson & Chiarucci 2000; Nicolson & McIntosh 2002).

Clements' view of community development is based on the premise of uniformity in the different types of stable or "climax" species associations, and that this uniformity is related to climate. Clements believed that the study of vegetation development should rest on the idea that the climax community "was an organic formation which arose, grew, matured, and died" (Crawley 1986). Each climax community was self-maintaining, self-reproducing and stable, so the community could repeat the development processes for an undetermined amount of time. In this view, community "life history," while complex, has definite and predictable processes analogous with the life history of an individual plant. To him, succession meant a dynamic equilibrium, including different processes and stages such as, nudation, migration, establishment, competition, reaction and stabilization

Gleason's "individualistic concept" was in sharp contrast to Clements' view of plant associations. Gleason recognized plant associations in vegetation. In his view, however, communities were not uniform entities; rather, they varied with space and time mainly because of chance and environmental factors. Vegetation units for Gleason were a temporary and fluctuating phenomenon dependent in its origin, structure and disappearance on the influence of the physical environment on the individual species and the nature of the surrounding vegetation (Crawley 1986; Barnes et al. 1998).

Gleason's individualistic view stressed the heterogeneity of community structure and essentially considered every species as a law unto itself. A particular species' distribution in space depends upon its individual peculiarities of migration and its environmental requirements. This individualistic view minimizes the importance of emergent properties attributed to plant communities by Clements.

These contrasting views lead to alternative ideas about the processes controlling plant community structure. For example, under the deterministic view, the number of species in a community is limited by the number of guilds (species sharing the same resources) present and the number of species per guild. The assumption of highly integrated structure implies that the presence of one species in a community is strongly influenced by the presence or absence of other species (Watkins & Wilson 1992). According to Keddy & Weiher (1999), E.C. Pielou's attempt in the 1970s to explain plant distributions along gradients was the first evidence that communities occur in discrete rather than random-individualistic associations.

On the other hand, in Gleason's individualistic view, while interactions occur between species, they are not strong enough to create any particular stable taxonomic assemblage of species that allows for competitive exclusion or even prevents the invasion of other species (Wilson 1989a). It follows that the species present at a given site are the result of their ability to disperse, establish and withstand the physical environment. It is suggested that chance substantially influences species composition, particularly in tropical rain forests (Hubbell & Foster 1986) but also in temperate plant communities (Wilson 1989a).

Community ecology and, in particular, the study of community structure continue address questions relating to how communities are put together and persist through time. This topic has been one of the most explored in ecology, and a review of recent papers makes evident that there is much left to explore (Keddy & Weiher 1999; Wilson & Chiarucci 2000; Nicolson & McIntosh 2002).

Underlying patterns in community ecology have been sought in interactions between species, assembly rules and in associations between species and the environment (Wilson 1999). One way to explore possible trait-environment relationships is in the search for plant functional types; that is, the set of plants that have similar responses to environmental conditions irrespectively of the species (Diaz et al. 1999b). Functional traits ultimately are the measurable attributes that define plant functional types.

Assembly rules

The search for "rules" to explain patterns in plant communities has recently received a great deal of attention by many community ecologists. The challenge to community ecologists is to predict composition of ecological communities given the pool of available species (Weiher & Keddy 1999); this is in contrast to evolutionary ecologists whose challenge is to determine how the species pool was formed (Figure 1).

Assembly rules are not "recipes for building communities" (Weiher & Keddy 1999). In contrast to the idea that assemblages are the result of individual species' responses to the environment, assembly rules represent a set of constraints on how species can come together to form assemblages (Weiher & Keddy 1999). Thus, assembly rules are simply about constraints on composition and are assumed to describe the patterns that result from the underlying mechanisms responsible for the processes responsible for these constraints (Wilson 1999). Assembly rules might, for example, influence the sequence in which species or groups of species are incorporated into the community based on the characteristics of species already present.

Evidence for assembly rules have been sought using various approaches ranging from null models to gradient analysis, and they have been expressed on the basis of: species abundance (e.g., biomass constancy, relative abundance); presence/absence (e.g., variance in richness, local versus regional richness, large-scale distribution); the position of a particular species along an environmental gradient; and plant characteristics (e.g., texture convergence, limiting similarity, guild proportionality) (Wilson 1999).

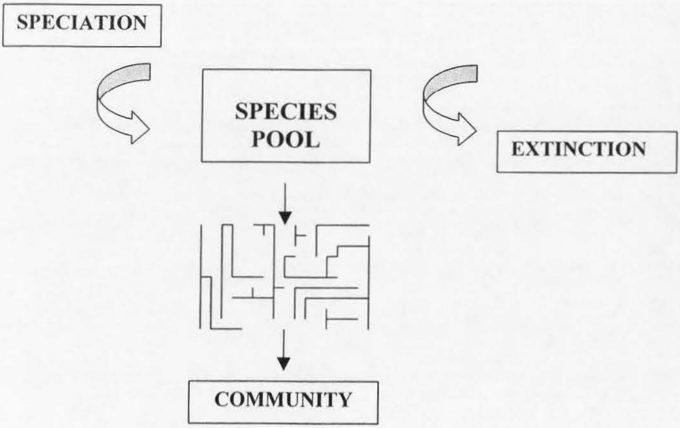


Figure 1. Assembly rules are implicit in the 'puzzle' of how species become part of a community; evolutionary ecology relates to the processes of speciation and extinction, i.e., formation of the species pool. Modified from Weiher & Keddy 1999.

While null models can provide insight into community structure, it is difficult to define assembly rules on this basis alone. Guilds and species traits may provide considerable additional insight. Explicit definition of assembly rules may be possible through the analysis of groups of functional traits. Patterns found in assemblages can be used as assembly rules if they generate accurate predictions.

Plant functional traits and types

A common objective in community ecology is the search for consistent and predictable associations in plant traits, types of plants and environmental conditions. Such generalizations would address a wide range of questions relating to natural ecosystems. It is assumed that specialization by plant species should result in identifiable groups of traits or plant functional types. Implicit in the use of functional types and traits is the assumption that they are directly or indirectly related to specific community and ecosystem processes. Additionally, it is assumed that the ability to account for processes in the ecosystems will facilitate the study of species diversity in natural ecosystems.

A common approach has been to seek consistent associations between groups of plant traits and environmental conditions, independent of the actual species involved (Keddy 1992). The term "character-based" was used by Orloci (1991) to imply species-free; taxonomy is intrinsic through the particular traits being considered. These sorts of trait-environment associations provide an opportunity to compare and predict responses of different floras or the behavior of a species not currently a part of the regional species pool, e.g., a potential invader (Wilson et al. 1994). As an alternative to classifications based on species, functional (i.e., trait-based) classifications may also have utility in describing the structure and functioning of ecosystems (Orloci 1991).

Classifications based on traits may provide important insight into the mechanisms underlying vegetation response (McIntyre et al. 1999). Perhaps the earliest use of this approach was by Theophrastus (ca. 300 B.C.) in which he classified individual plants as trees, shrubs and herbs (Gitay and Noble 1997; Weiher et al. 1999). Character- or trait-based descriptors were central to early vegetation studies concerning the environmental fitness and survival of plants (Humboldt 1806; Kerner von Marilaun 1864; Warming 1884; Raunkiaer 1907; as described by Orloci 1991)

Functional classifications have been put to a wide range of uses, including: dynamic models of global vegetation; schemes describing functional response of a regional flora to environmental factors; schemes addressing specific disturbances; empirical landscape models; stand/community models; trait-environment relationships; searches for functional groups of species responding in a similar way to environmental conditions; assembly rules; comparative ecology; evolutionary approaches to comparative ecology; meta-population dynamics; phenotypic plasticity within populations; ecophysiology and the mechanistic understanding of plant response to the environment (McIntyre et al. 1999; Weiher et al. 1999)

Despite broad application, functional classifications have limitations. For example, the utility of functional classifications in climate-change modeling may be limited by the fact that some future combinations of environmental factors may have no currently existing counterpart. On the other hand, "the analysis of present spatial patterns is a useful heuristic tool in trying to predict the direction (and to a lesser extent magnitude and rate) of vegetation change under shifting climate," providing an empirical support to modeling efforts at the regional scale (Diaz et al. 1998).

Different traits have been associated with various community and ecosystems processes. A list of "core" traits has been proposed by Weiher et al. (1999) based mainly on three general life stages of plants: dispersal, establishment and persistence (Table 1).

Table 1. Core trait list proposed by Weiher et al. (1999) based on dispersal, establishment, and persistence of individuals in the community.

Trait	Function
Seed mass	Dispersal distance, longevity in seed bank, establishment success, fecundity
Seed Shape	Longevity in seed bank
Dispersal type	Dispersal distance, longevity in seed bank
Clonality	Space acquisition
Leaf Water Content (LWC),	Relative Growth Rate (RGR), plasticity,
Specific Leaf Area (SLA)	Stress tolerance, evergreenness, leaf longevity
Height	Competitive ability
Above Ground Biomass	Competitive ability, fecundity
Life history	Plant longevity, space-holding ability, disturbance tolerance
Onset of flowering	Stress avoidance, disturbance avoidance
Resprouting ability	Disturbance tolerance
Stem density	Plant longevity, carbon storage

Diaz et al. (1998) consider vegetative traits related to leaves such as size, turnover, longevity and chemical composition to be associated with processes like productivity, nutrient cycling and carrying capacity. On the other hand, they suggest that traits related to regeneration, such as seed output, dispersal mode and seed persistence, are indicative of stability, recolonization after major disturbances and migration over the landscape. Diaz et al. (1999b) also present an extensive bibliography related to traits and ecosystem processes (Table 2).

In any trait-based study of plant communities, the potential number of traits is essentially limitless and must be constrained by the specific objectives of the study (McIntyre et al. 1999). Ideally traits will capture important functional and structural attributes of the species; however, data on some potentially desirable traits may not be attainable.

The observation that many functional traits are closely associated with plant morphological characteristics is taken as evidence of the positive relationship between form and function (Weiher et al. 1998). Further, the existence of trade-offs among traits is taken to indicate that a relatively few simple morphological traits may be adequate to express a species' functional attributes (Weiher et al. 1998). Because of the differing objectives in individual studies, it is neither possible nor desirable to have strict standardization for the selection of traits. However, it is desirable to have at least a common language relating to traits for purposes of comparison and tests of repeatability in different regions of the world as a response to disturbance processes (e.g., fire, grazing and land use change) (McIntyre et al. 1999).

Table 2. Traits and processes considered in some of the literature (after Diaz et al. 1999b).

Trait	Community/Ecoystem Processes	Source
Relative growth rate	Productivity	Grime et al., 1988; Shaver et al., 1997
Leaf turnover rate	Nutrient cycling	Schulze & Chapin, 1987; Nadelhoffer et al., 1991; Reich et al., 1992; Shaver et al., 1997
Nutrient content	Production, Nutrient cycling	Reich et al., 1992; Swift et al., 1979; Aber & Melillo, 1982; McClaugherty et al., 1985; Schulze & Chapin, 1987; Hobbi, 1992
	Carrying capacity for herbivores	McNaughton et al., 1989; Harris, 1991; Shaver et al., 1997
Biomass	Flammability	Chistensen, 1985; Dublin et al., 1990
Lifespan	Inertia	Richardson & Bond, 1991; Chapin et al., 1993
Canopy structure	Aerodynamic conductance	Jarvis & McNaughton, 1986; Kelliher et al., 1993
	Interception, water relations, runoff	Calder, 1990; Woodward & Diament, 1991; Holling, 1991; Kelliher et al., 1993
	Roughness/albedo	Schulze & Zwolfer, 1994
	Temperature buffering	Schulze, 1982; Holling, 1991
	Soil stability	Holling, 1991
Secondary growth	Carbon sequestration	Larcher, 1995; Schulze, 1982
Ramification	Structural complexity	Lawton, 1983, 1987; Brown, 1991; Marone, 1991
Root architecture	Water uptake	Woodward & Diament, 1991; Kelliher et al., 1993; Sala et al., 1997
Reserve organs	Resilience	Grime, 1979; Noble & Slatyer, 1980
Pollination mode	Expansion over landscape	Faegri & van der Pijl, 1979; Schulze & Zwolfer, 1994
Persistent seed bank	Resilience	Thompson & Grime, 1979; Thompson et al., 199
Seed number	Expansion over landscape	Noble, 1989; Hodgson & Grime 1990
Dispersal mode	Expansion over landscape	Howe & Samllwood, 1982; Noble, 1989; Hodgson & Grime,1990
Presence of root symbionts	Diversity	Grime et al., 1987; Gange et al., 1990
	Nutrient cycling,	McNaughton & Oesterheld, 1990
	Rate of Succession	Amaranthus & Perry, 1994

CHAPTER 3

A CONCEPTUAL MODEL OF COMMUNITY STRUCTURE

This simple model is intended to represent the vertical structure of different plant communities. Individuals are grouped based on life forms assumed to be broadly associated with important traits such as plant size (Lavorel et al. 1999b). Life forms have commonly been used in classifying communities. For example, Theophrastus (ca. 300 B.C.) classified plants as trees, shrubs or herbs based mostly on the presence or absence of woodiness in the stems (Gitay & Noble 1997; Weiher et al. 1999).

A single group or stratum is the simplest community in my model. The group is formed of annual and/or perennial grasses and herbs and is called the grass functional group (GFG). Figures 2 and 3 include a community, the grassland functional type (GFT), consisting of only the grass functional group.

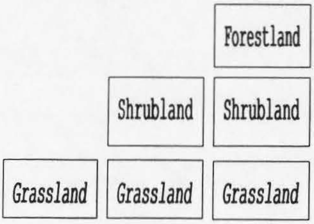


Figure 2. Conceptual model describing the way communities can be structured internally based on life forms.

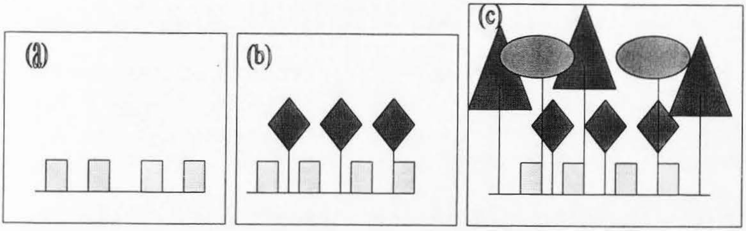


Figure 3. Schematic representation of (a) grassland, (b) shrubland, and (c) tree plant functional types.

Adding a new layer, represented by the shrub functional group, results in a new type of community, the shrub functional type (SFT). This community consists of two layers, the dominant or top one with mostly shrubs (SFG) and the lower or bottom one with grasses and herbs (GFG). The most structurally complex community is represented by three strata or functional groups; a tree functional group (TFG) at the top, an intermediate layer represented by the shrub functional group and the grass functional group at the bottom.

In this conceptualization, functional type is analogous to community or vegetation type and is defined by the relative abundance of life forms. The functional group represents those species within the functional type that have similar life form. Therefore, the model assigns communities to one of three functional types, each with between one and three functional groups. Characterization and assessment of the groups and types is based on functional traits as opposed to the traditional use of species.

This conceptual model provides the framework for an analysis of the internal structure of plant communities based on functional traits. The model is used to organize general research questions. For example, are there sets of functional traits consistently associated with, and which can be used to distinguish between, the various functional groups and types? Are there trends or patterns in traits within and between functional types and groups? These general questions will be addressed through a descriptive analysis of quantitative and qualitative variables between and within functional types.

CHAPTER 4

STUDY SITES

Two phylogenetically and environmentally contrasting sites were selected to evaluate trait-based classifications and the distribution of traits within and between communities. Camp Williams is a Utah National Guard training installation located in a semidesert region of low potential productivity. Camp Grayling is a Michigan National Guard training installation located in a temperate mixed forest region of considerably higher potential productivity (Table 3).

Table 3. General description of the two different ecoregions used in the research.

Variable	Camp Williams, UT	Camp Grayling, MI
Ecoregion[1] (Province)	Intermountain Semidesert and Desert	Laurentian Mixed Forest
Extension (ha)	10, 000	60, 000
Elevation (masl)	1300-2200	0-730[2]
Mean Annual Temperature (° C)	5-12	2-10[2]
Mean Annual Precipitation (mm)	250-500	610-1150[2]
Soils	Mollisols, Aridisols, Inceptisols	Spodosols, Histosols
Floristic composition (number of species)	400	866

(1) Bailey (1995)

(2) Information from Bailey's Province description.

Camp Williams, Utah

Location. The 10,000 hectares of Camp W.G. Williams are located in north central Utah. 40 km south of Salt Lake City (Figure 4). Camp Williams is located on the east slope of the Traverse Mountains with the Oquirrh Mountains to the west and the Wasatch Mountains to the east (Integrated Natural Resource Management Plan (INRMP 2001). Camp Williams includes portions of Salt Lake and Utah Counties.

Regional ecosystem classification. The Ecoregion hierarchical classification identifies domains, divisions, provinces and plant communities based on climate and vegetation (Bailey 1995). This classification is useful for planning and implementing ecosystem management (INRMP 2001) since the abiotic and environmental factors used to define ecoregions (climate, physiography, soils, hydrology and potential natural communities) regulate the structure and function of the ecosystems. Camp Williams is located in the Temperate Desert Division (Figure 5) and, more specifically, the Intermountain Semidesert and Desert Province (Bailey 1995). The province includes the Great Basin and the northern Colorado Plateau in Utah. Lower parts of basins have alkaline and saline salts (e.g., salt flats). Average annual temperatures ranges from 4° to 13° C with annual precipitation from 130-490 mm, often in form of winter snow. Rain can occur during summer months especially at high elevations (Bailey 1995).

Lowland areas are dominated by sagebrush or other plants tolerant of alkali and poorly drained soils like Aridisols. At higher elevations there is typically a woodland zone dominated by combinations of pinyon pine and juniper species. Above this woodland zone, forest zones dominated by ponderosa pine, Douglas-fir, or

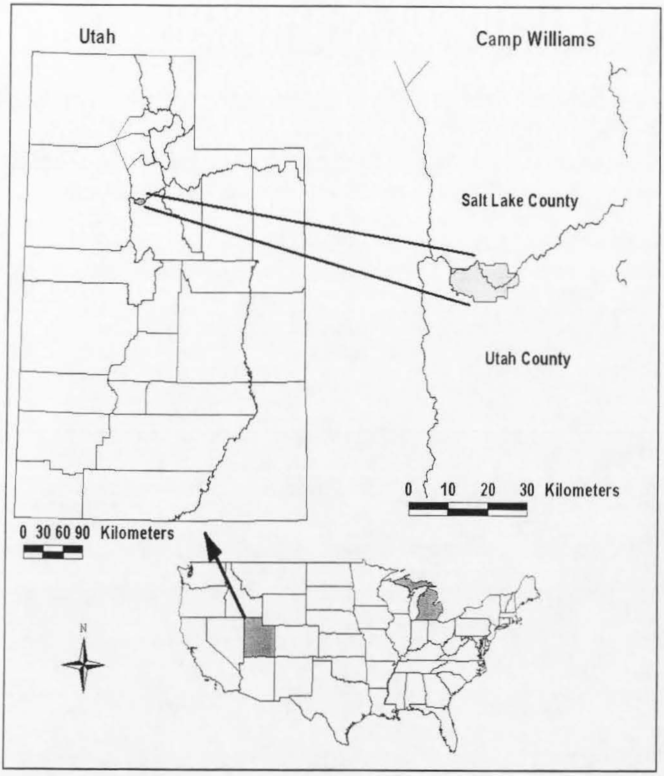


Figure 4. Localization of Camp Williams, Utah

subalpine fir and Engelmann spruce typically occur at successively higher elevations. Elevations at Camp Williams are not sufficient to support any of the forest zones and the woodland zone is dominated by juniper and Gambel oak.

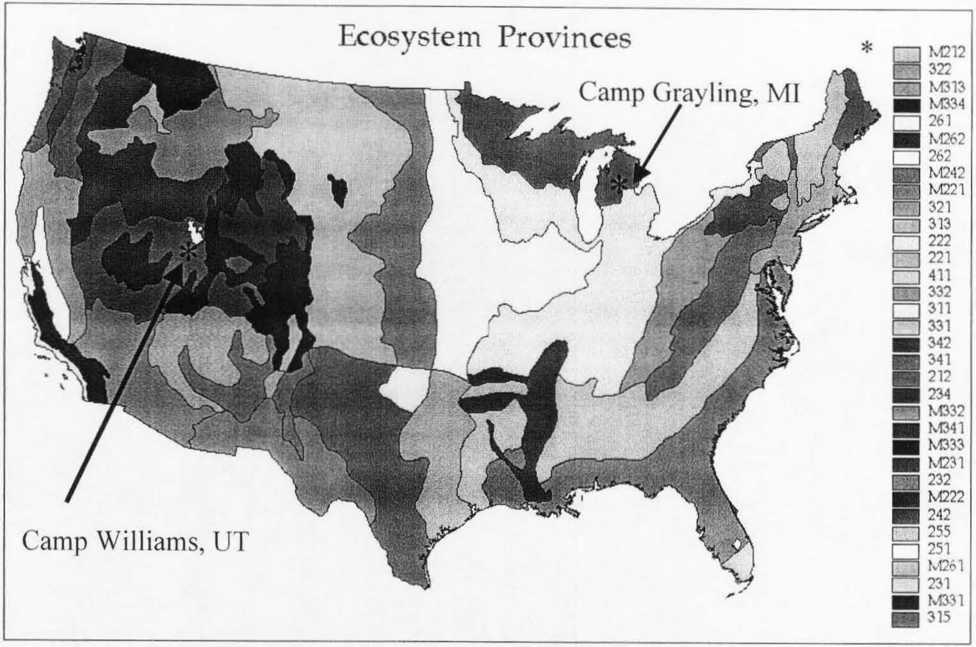


Figure 5. Ecosystem provinces of the United States *(Refer to Bailey, 1995)

Topography. The eastern half of Camp Williams is stratified by east-west drainages; the western half of the installation has north-south drainages. This physiography produces patterns in vegetation distribution related to slope and aspect (INRMP 2001). Elevation ranges from 1300 to 2200 m, and the slopes range from gentle to 58 degrees.

Climate. Camp Williams has a continental climate characterized by low precipitation and drastic fluctuations of temperature between summer and winter. The average annual precipitation ranges from 250 to 500 mm, depending on elevation, mainly in the form of winter snow and rain early summer. Annual average temperatures are between 5 – 12° C. Hot summers with extended droughts and cold winter temperatures influence species establishment, especially the cold season species that grow during spring (INRMP 2001).

Soils. Parent material at Camp Williams is derived from quartzite, limestone, sandstone, granite, andesite and conglomerate. The soils are representative of three soils orders: Mollisols, Aridisols and Inceptisols. In general, the soils have good to excessive drainage with textures from silt loam and clay loam.

Vegetation. Camp Williams represents a transition from montane forest to juniper woodland in the Basin Range Province. There are six major vegetation cover types identified from satellite imagery. These types include: sagebrush communities, grasses and herbs, bare/annual weeds and bare agricultural, oakbrush/sagebrush/grass mixed communities, oakbrush communities, and juniper woodlands. A total of 400 vascular species have been identified on the installation; a quarter of these are introduced species represented by grasses and herbs (Albee et al. 1988; Shultz & Hysell 1996).

Disturbance. Camp Williams has a long history of grazing by cattle and sheep. Fires of high intensity are frequent; these are often associated with the military training. Impacts of training activities on soil, water, and wildlife are fairly modest since the high impact practices such as antitank attacks, ditching, demolition, firing points, ranges, and bivouac areas are restricted to either hardened or naturally resistant sites (INRMP 2001). Other potential impacts include off-road traffic and the introduction of noxious weeds.

Camp Grayling, Michigan

Location. Camp Grayling is located in the northern portion of Michigan's lower peninsula. The installation has 60,000 ha and includes portions of Crawford, Kalkaska, and Otsego counties (Figure 6).

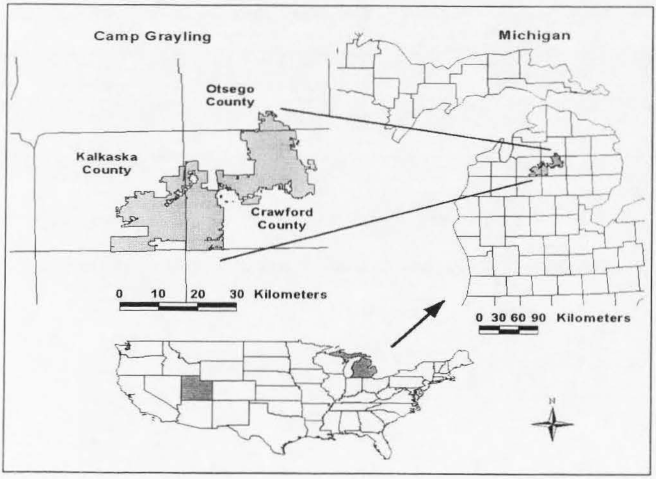


Figure 6. Location of Camp Grayling, Michigan.

Ecosystem classification. Camp Grayling belongs to Bailey's (1995) Warm Continental Division and the Laurentian Mixed Forest Province (Figure 5). The region has generally low topographic relief. Glacial features from the Pleistocene are common. Elevation ranges from 0-730 m. Winter is long and severe with a frost-free season of 100 to 140 days. Average annual temperature ranges from 2° – 10°C and an average annual precipitation of 610-1150 mm during summer (Bailey 1995).

The province is considered transitional, since it lies between the boreal forest and the broadleaf deciduous forest. Conifers often pioneer on sites with poor soils (Bailey 1995).

The Laurentian Mixed Forest Province has a variety of soils. These include peat, muck, marl, clay, silt, sand, gravel and boulders in different combinations.

Topography. Camp Grayling has around 28,000 ha of outwash plains and 32,000 ha of moraines. Moraines form the higher ridges at the installation. There are many lakes resulting from large glacial ice blocks left to melt after glacial retreat at the end the last ice age (Patraw 1997).

Climate. The lower peninsula of Michigan has a severe climate with an average of 115 days of growing season during the year. Due to the lack of moderating influence from the Great Lakes, the region has great variations in climate during spring and fall (Patraw 1997).

Soils. Advances and retreats in the Pleistocene formed the spodosols and histosols that predominate at Camp Grayling. Sand and low nutrient content characterize the areas of outwash plains (Patraw 1997).

Vegetation. There are five major community types: (1) pine forest in the outwash plains with jack pine, red pine and white pine forest, and oak species, (2) mixed-hardwood forests on the moraines with maple, hemlock, beech, and birch, (3) balsam forest with balsam fir, black spruce, paper birch, trembling aspen, and bigtooth aspen, (4) second growth forests of aspen and paper birch, and (5) wetland communities with black spruce and tamarack and swamp forests of white cedar, balsam fir, hemlock, birch, and maple (Daniel & Sullivan 1981 in Patraw 1997). The total number of vascular species reported in the floristic survey is 866 species of which approximately 15% are introduced grasses and herbs.

Disturbance. Camp Grayling is a major military training center for air and tank exercises (Patraw 1997). In addition to disturbances associated with military training, there are natural disturbances such as wildfires. Recreational activities also take place in the area and include activities like hunting, fishing, and snowmobiling.

CHAPTER 5

METHODS

Plot data

LCTA data. The U. S. Army and Army National Guard Bureau have implemented an Integrated Training Area Management (ITAM) program (Patraw 1997). One of the five basic components of ITAM is the standard Land Condition-Trend Analysis (LCTA) monitoring program. This program was first implemented in 1984 at Fort Carson, Colorado, and Fort Hood, Texas; LCTA was recommended for Army-wide implementation in 1987 (Tazik et al. 1992).

The LCTA program is a standard method for the inventory and monitoring of flora, fauna and land use (Tazik et al. 1992). It is intended to provide a baseline for managers and decision makers regarding natural resources conditions and trends. It is also intended to allow evaluation of different management practices implemented at the training installations (INRMP 2001). LCTA monitoring methodology uses permanent field plots based on stratified random sampling (Tazik et al. 1992)

A basic LCTA plot consists of a 100-meter vegetation transect monitored annually. The plots are distributed, roughly in proportion to area, in the different vegetation types present at an installation. For each plot, a 100-meter line transect is measured for ground cover, canopy cover and surface disturbance at 1 meter intervals. A 6 meter by 100 meter belt transect is measured for density of plant species (INRMP 2001). Details regarding plot establishment and field methods are provided by Tazik et al. (1992).

Data acquisition. LCTA information for different years and installations was available for this research. Since this study was not intended to consider dynamic analysis of community structure, a single season's inventory was used. Camp Williams and Camp Grayling were chosen as representing substantially different climates and ecoregions (Bailey 1995).

Preliminary analysis for six continuous years of LCTA inventory (1993-1998) from Camp Williams permitted detection of inconsistencies or incomplete files and also led to the decision to discard the first and last year of data inventory. This was done to avoid first time implementation errors and the most recent adjustments in field measurement techniques. Data from the 1995 Camp Williams survey were used; this included 67 line transects (plots). Camp Grayling LCTA data for 1992 were used and these data were supplemented with data for additional plots measured in 1993 in order to fully represent all of the functional types. In total, 82 line transects (plots) were included in the Camp Grayling dataset.

Two basic information sources from LCTA were used in this research. The first is the LCTA data for the species-specific canopy cover data. The second is the results of the comprehensive floristic survey carried out for both installations. Tables A.1 and A.2 in the appendix include examples of the data file structure for both the line transect data and the floristic survey data. The floristic data file includes vegetation type, family, genus, species, life form, life span, origin, and common name.

The line transect data (referred to as "Aerial Coverage" in the LCTA protocol (Tazik et al. 1992) includes: (1) plot identification; (2) species identification; (3) location of the individual plant along the 100-m line transect (sample of 100 points starting at 0.5

m and then at 1-m intervals); (4) its height measured at decimeter intervals up to 2 m, for individuals taller than 2 m height was recorded in 0.5 m intervals up to 8.5 m. My work only uses the maximum height reported for a given species at each 1 m interval ; these data were used to reflect the frequency of species and, ultimately, the frequency of functional traits by plot.

Trait Selection

To analyze the internal structure of communities based on functional traits, a species-by-traits matrix was constructed. Species frequencies, determined from the line transect data, were identified and combined with the information from the floristic survey. The result was a matrix of sampled species and some of the traits included in the floristic data (life form, origin, life span, and species identification).

Construction of the species by traits matrix followed the scheme proposed by McIntyre et al. (1999) to develop a list of traits, the "list of core traits" by Weiher et al. (1999) and the recommendations of Keddy (1992), Diaz et al. (1998, 1999a), Box (1995), Kelly (1996), Reich et al. (1999), Flemming (2000), Kennedy et al. (2000) and Lavorel et al. (1999b) concerning relevant plant functional traits.

McIntyre et al. (1999) suggested an initial trait list that passes two different filters: selection of traits to be measured and selection of traits to be analyzed. Selection of traits for the initial list and the ones to be measured was intended to be a group of functional traits that implicitly reflected possible ecosystem functions and/or processes. In terms of practicality, they needed to be easily found in bibliographic sources since it was not feasible to determine them by direct observation or measure.

In this research, a species' functional traits were assigned using appropriate published regional and expert sources of information; direct inventory of functional traits through field inventory was not done. The availability of published information regarding traits was an important criterion in reducing the number of the initial list (Figure 7). If a survey of the floras and another sources revealed a lack of information reported for a particular trait, then that trait was eliminated from the list of functional traits to be considered.

For example, specific leaf area, leaf water content, leaf hairiness, number of seeds per plant or fruit, or seed mass were not considered because information of these traits was not included in the LCTA data nor is it typically reported in published floras. Also, some functional traits are included in the recommendations of various authors to reflect a specific disturbance effect (fire, grazing, etc.); since this was not an objective of my research, these types of traits were also eliminated (e.g., canopy structure, lateral spread, secondary compounds, silification, sclerophylly).

Some of traits are highly correlated and reducing the list of traits to be measured still allows broad general deductive analysis. For example, carbon immobilization in support tissue or photosynthetic metabolism (CAM versus C3 or C4) can be related to life forms (Diaz et al. 1999a). Similarly, breeding form (dioecious, monoecious) can be inferred from the taxonomic information (Gitay et al. 1999).

Finally, the trait list recommended by McIntyre et al. (1999) can include examples of a functional trait referred to by different names by different authors. For example, stem density (woody, non-woody) (Weiher et al. 1999), stem tissue type (succulent,

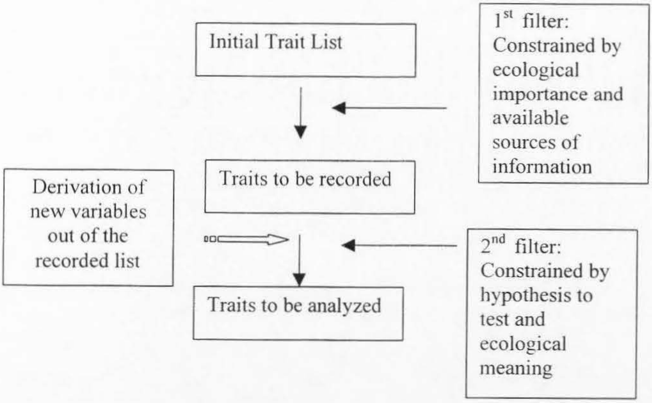


Figure 7. Diagram showing stages followed to select traits in Camp Williams, UT, and Camp Grayling, MI. Modified from McIntyre et al. 1999.

herbaceous, woody) (Pillar 1999); life history (annual, biennial, perennial versus life span) (Campbell et at. 1999; Weiher et al. 1999; Diaz et al. 1999a; McIntyre et al. 1999).

Some of the traits were inferred from the flora information when it was not possible to determine them directly. For example, pollination and seed dispersal were inferred. Conspicuous and brightly colored petals were assumed to be indicative of animal pollination; absence of color was taken to imply pollination by wind. Seed dispersal was inferred by the kinds of dispersal structures (e.g., wings, prickles). For example, small-winged seeds were considered to be wind dispersed. A taxonomic expert confirmed classifications of pollination mode and seed dispersal (Shultz pers. comm.). Published sources consulted included: Fernald (1950); Radford et al. (1968); Schopmeyer (1974); Cronquist et al. (1984); Burns & Honkala (1990); Welsh et al. (1993); Shultz & Hysell (1996); Baskin & Baskin (1998); Magee & Ahles (1999).

The final list of traits used in the analysis (Table 4) includes 11 qualitative and three quantitative traits; there are between two and 12 classes per trait for a total of 75 classes. The qualitative variables were transformed into categorical scales for the analysis. The data were analyzed as frequency of functional traits by class by plot and as proportions of specific traits per plot.

Aditional variables considered. Variables calculated for each plot were: cover, species richness, species diversity, and trait diversity. Cover was expressed as the frequency of intercepts or "hits" in the 100 m transect. Richness represents the number of species present on the plot. Both were obtained from the aerial coverage files.

Species diversity index was calculated using Shannon's index (H'). This index has the property of H'=0 if and only if there is one species in the sample, and H' is maximum only when all the species (S) are represented by the same number of individuals (i.e., intercepts), a perfectly even distribution of abundance (Ludwig & Reynolds 1988).

Species diversity by plot was calculated with the formula:

$$H' = \sum^{S}_{i=1}\left[(n_i/n)\ln(n_i/n)\right]$$

where H' is the Shannon's diversity index, n_i represents total frequency of the *i*th species in the plot and n is the total frequency by plot.

In an analogous way, a trait diversity index was calculated using the Shannon's formula, including four traits: life form, life span, seed dispersal, and pollination mode.

$$T' = \sum^{S}_{i=1}\left[(n_i/n)\ln(n_i/n)\right]$$

Table 4. Traits considered by species in Camp Williams, UT and Camp Grayling, MI

Trait	Classes
Life Span	Annual Perennial
Life Form	Grass Herbs Shrub Tree
Origin	Native Introduced
Leaf Type	Simple Compound
Leaf Shape	Elliptic Needle Fleshy Lanceolated Linear Oblong Ovate Oblovate Pinnately Wedge
Fruit Type	Achene Berry Capsule Utricle Caryopsis Cone Nut Nutlet Samara Sori Pod Schizocarp
Seed Dormancy Type	Non-dormant Morphological Physical Physiological Morphophysiological
Seed Dispersal	Wind Insects- Animals with low mobility (ants, beetles, rodents, etc.) Animals with high mobility (large mammals, birds, etc.)
Pollination Mode	Wind Animal
Vegetative Spread	Present Absent
Flowering Length Period	Spring-Fall Spring-Summer Summer-Fall Spring-Winter Spring Fall Winter
Maximum Leaf Size (cm)	< 1.0 1.0-15.0 15.0-30.0 > 30.0
Maximum Seed Size (mm)	< 10.0 10.0-30.0 30.0-50.0 > 50.0
Maximum Total Height (m)	< 0.5 0.5-1.0 1.0-1.5 >1.5

where T' is the trait Shannon's diversity index, n_i is the class' trait frequency for the *i*th species and n is the total class' frequency on the plot. Life form and life span are reported as two important variables to define *a priori* communities (Lavorel et al. 1999b) and are indicative of persistence of a plant community. In addition, they can be related to competitive ability and species longevity. Seed dispersal and pollination mode were included because of their ecological relevance in the dispersal and establishment processes of a community (Weiher et al. 1999), and also for their presumed effectiveness in contrasting the structure of communities. The final trait list used in the analysis is presented in Table 4.

Several data matrices were constructed for the analysis. The species by trait matrix (S) was expanded into a species-by-trait class matrix (C), and this multiplied by the plot-by-species frequency matrix (P) representing the basic line transect data. The resulting plot-by-trait class frequency matrix (N) represents the basic data used in the trait-based community classification and analysis of the internal trait-based structure of communities. The N matrix is an expression of communities' trait classes; this differs from most previous studies, in which a species-by-trait matrix is used and then assessed with respect to different disturbance regimes or environmental factors. The N matrix represents the basic information used to describe and analyze the regional distribution and internal structure of communities. The information was not to be related explicitly to environmental factors (Figure 8).

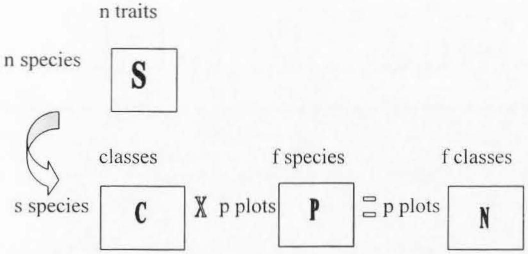


Figure 8. Representation of data matrices generated.

Trait-based community ordination and classification

Correspondence analysis (CA) is a classic and simple approach for ordination commonly used to summarize associations between a set of categorical variables in a small number of dimensions. Relationships among categories are used to interpret similarity patterns (SAS 1990). The CA analysis was done using the Statistical Analysis System (SAS) package and in particular the CORRESP procedure and GPLOT macros to generate biplot graphs SAS (1990).

The plot-by-trait class matrix was used to obtain a trait-based ordination of the plots in an axis system and the set of associated classes to determine that ordination. Initially the ordination was based on a subset of traits (life form, life span, seed dispersal and pollination mode).

Object scores represent distances between plots/functional types in multivariate space. In general, objects that are close to each other are more similar than those further apart. Attributes with a high influence for discrimination contribute most to the distances between objects in that dimension (Sutherland et al. 2000).

Rather than a conventional ordination of plant communities on the basis of species abundance, the ordination of plant communities/functional types was based on relative abundances of traits. This procedure was exploratory and intended to find if there was a clear definition of vegetation/functional types at a regional (installation) level. It was not intended to directly relate ordination results to particular environmental conditions since this information was limited and beyond the scope of the research.

An objective of the research, once the set of traits was identified, was a detailed analysis within and between the functional types to address the following general questions: Are there sets of traits that define the different functional types? Are there sets of traits that define functional groups within a community? If so, are these traits similar for the same functional groups in different functional types? Are there trends or patterns for traits within a functional type?

Internal structure

Two different steps in the *a priori* classification of functional types were applied to the data. Figure 9 illustrates the first step communities were classified into functional types (grassland, shrubland and forest) based on of life-form frequency. The second step defines functional groups (grasses/herbs, shrubs and trees) on the basis of similar life forms. Similar *a priori* approaches have been used by others: Pillar (1999) used species height to define the number of strata depending on the elevation range of the sites;

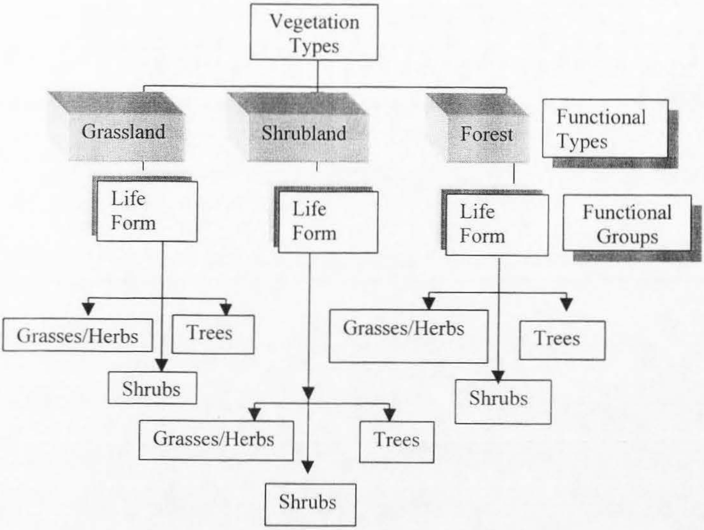


Figure 9. Steps to classify vegetation types into plant functional types based on life form.

McIntyre et al. (1999) and Lavorel et al. (1999a) defined five groups of species based on growth form and life cycle in a herb-dominated vegetation; Gitay et al. (1999) classified rain-forest species as trees, shrubs and vines based on morphological traits and then used only trees to characterize functional types; Hadar et al. (1999) defined 10 functional groups based on a combination of life forms and taxonomic groups in Mediterranean communities; Landsberg et al. (1999) used life form and species composition to categorize understory flora in arid rangelands; Skov (2000) used vegetative attributes (Raunkiaer life-form and height of adult plants) and regenerative attributes (dispersal mode and pollination class) to investigate the distribution of plant functional attributes.

The main objective of using *a priori* classifications and, in particular, classifications based on life forms is to identify different set of traits across the life forms (Lavorel et al. 1999b).

The LCTA data associated each plot with one of the six or five major vegetation types in Camp Williams and Camp Grayling, respectively (Table 5). The original LCTA classifications, however, were not completely accurate. When examined in detail, some plots might, for example, be identified as grassland but were dominated by shrubs, or a plot identified as a pine forest was mostly occupied by grasses. In part, this was because they were classified based on satellite imagery. For this reason, and to get a more general and integrative description of the communities, criteria based on percentage of life forms was applied to each of the plots in order to reclassify them accordingly to the conceptual model (Figure 2).

Table 5. Classification of Vegetation Types for Camp Williams, UT, and Camp Grayling, MI

Installation	Vegetation Type Classification (LCTA)
Camp Williams	Sagebrush Grasses and Herbs Bare/Annual weeds and bare agriculture Oakbrush/Sagebrush/Grass mixture Oakbrush Juniper woodlands
Camp Grayling	Pine forest Mixed-hardwood forest Balsam forest Second growth aspen and paper birch forest Wetland communities and swamp forest Grassland Upland and Lowland brush

For Camp Williams, a community type was classified as a forest (analogous to woodland) if trees contributed at least 10% cover for the plot. If shrub cover was greater than perennial grasses, then a plot was classified as Shrubland. Coverage of perennial grasses of at least 40% and shrubs less than 20% constituted a grassland.

For Camp Grayling different criteria were used. Even when it is recognized that different criteria in the definition of functional groups may confound the differences in climate.

If more than 50% cover on a plot was represented by grasses/herbs, shrubs or trees, then that life form group was considered to characterize the functional type (i.e., grassland, shrubland and forest, respectively). In situations where the cover of trees and shrubs together was 40% or greater, the plot was classified as a shrubland; these communities probably more closely resemble Camp Williams woodland plots.

The "conceptual community" used in the analysis is illustrated in Figure 9. The grassland functional type includes just the grass functional group; shrubland functional type has the grass and shrub functional group, finally, the forest functional type has a grass, shrub and tree functional group. This representation includes the dominant life forms and implies the sets of functional traits characterizing both the groups and types.

Trait relative proportion. The plot-by-trait class matrix was used to calculate class proportions. It was possible to assess the frequency for each class and relate this to the total frequency of traits by functional group functional type.

For example,

$$RCTF = Cf_i / \sum_{i=1}^{n} Cf_i$$

where RCTF is the relative class trait proportion, Cf_i is the class frequency for a particular trait, and Cf_i represents the summation of all class frequencies in a particular trait.

Hypotheses relating to functional types, functional groups and regions

A series of hypotheses were formulated based on the conceptual model. In Figure 10, hypotheses relating to differences between functional types are indicated with an A; hypotheses relating to differences between functional groups within the same community are indicated with a B; hypotheses relating to differences between different functional groups across the tops of difference functional types are indicated with a C; hypotheses relating to differences in a particular functional group within different functional types are indicated with a D.

A. As functional types increase in complexity (i.e., grassland to forest) there are increases in total cover, species diversity index, trait diversity, richness, wind pollination proportion and wind seed dispersal proportion.

B. Within a given functional type and moving from the top functional group to the bottom there are decreases in cover, the proportions of wind pollination, wind seed dispersal, seed size and the length of the flowering period. From the top functional group to the bottom there are increases in species diversity, trait diversity, richness, leaf size and the proportions of annuals, compound leaves and vegetative reproduction.

C. Functional groups at the top of simple to complex functional types create a gradient with increases in cover and the proportion of wind pollination and wind seed dispersal.

Along this same gradient there are decreases in species diversity, trait diversity and richness.

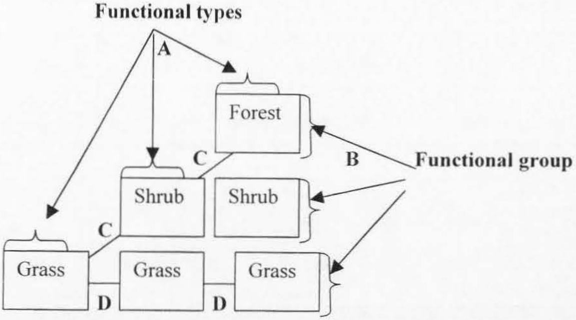


Figure 10. Schematic representation of the conceptual model and the groups used to formulate hypothesis.

D. The bottom functional groups, moving from simple to complex functional types, create a gradient with decreases in decrease richness, species diversity, trait diversity, cover and the proportions of wind pollination and wind seed dispersal.

In addition, it is hypothesized that total cover, as well as species and trait diversity increase for a given functional type in relation with a gradient in environmental conditions. Similarly, at the community level, it is expected that the proportion of wind seed dispersal increases from woodland to evergreen communities and the proportion of compound leaves increases with functional type complexity.

To address these hypotheses, differences in functional types and functional groups were assessed for the quantitative variables (richness, cover, species diversity, trait diversity, height, maximum leaf size and seed size) and for proportions in the qualitative variables.

Quantitative variables and proportions were analyzed using PROC ANOVA (SAS 1990) to test for homogeneity of means and proportions between and within functional types. Tests were considered under null hypotheses of no significant differences between means different functional types and groups. Results of this analysis represent an assessment of the internal associations between plant traits; consistent patterns will be suggestive of assembly rules.

CHAPTER 6

RESULTS

Ordinations of functional traits were conducted for both installations using Correspondance Analysis. Comparisons are made of ordinations based on the entire set of functional traits and ordinations based on a subset of core traits. These results are used to examine the sets of functional traits associated with the different functional groups. Finally, there is a detailed analysis of variance for quantitative variables within and between functional groups and types (vectors A, B, C and D).

Camp Williams

Appendix -Table A.3 shows the inertia and chi-square decomposition with six significant dimensions to explain the association between row and columns for the Camp Williams data. This ordination was done using Correspondence Analysis (CA) for life form, life span, seed dispersal and pollination mode. The first and second dimensions explain approximately 80% of the total chi-square and inertia (56% and 23% respectively). This is an indication that the relationship between row and columns (plot-classes) is mostly bi-dimensional.

Figure 11 is the biplot for the Camp Williams data. Life form is the trait discriminating in both dimensions. Grasses and herbs are located in the lower left quadrant; shrubs and then trees are arrayed towards the upper right quadrant. Functional types are also discriminated by seed dispersal (i.e., seed dissemination by big animals) and life span (i.e., annuals). The axis for Dimension 2 indicates that that besides life form

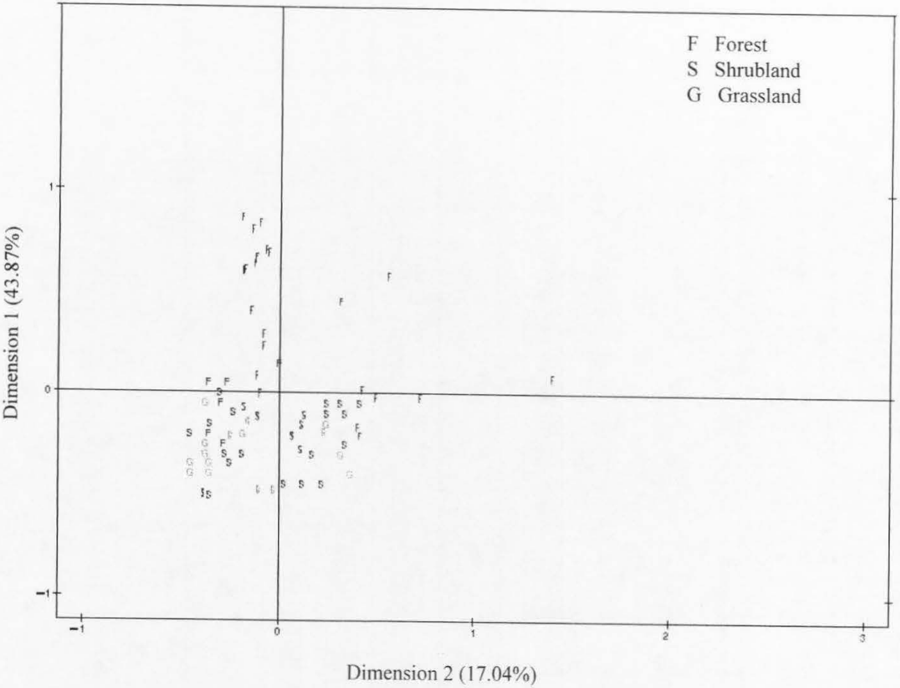


Figure 11. Biplot for correspondance analysis in the "core traits" for Camp Williams, UT.

(shrub), pollination mode (by animals) also separates functional types (Appendix -Table A.3).

Even without clear ordering of functional types, it is possible to distinguish the classes that discriminate two groups along the axis of Dimension 1. The first one includes perennial individuals with shrubs and trees that are mostly pollinated by wind and with seeds dispersed by animals. The second class is formed by annual grasses and herbs pollinated by animals and with wind dispersal of seeds.

Correspondence analysis using all of the qualitative traits for Camp Williams is illustrated in Figure 12. The ordination of functional types is less clear in this biplot because of the greater number of dimensions that contribute to the inertia and chi-square; Dimensions 1 and 2 explain 60%. It is still possible to distinguish that life form and life span segregate communities along Dimension 1; however, seed dormancy (morpho-physiological and morphological) contributes more to the ordination together with elliptic leaf shape and seed dispersal by big animals. Along Dimension 2, leaf shape (needle) and fruit type (cone) are the classes that contribute most to the inertia and chi-square (Appendix -Table A.4).

Camp Grayling

There are seven significant dimensions that help to explain the association of columns and rows in the data for Camp Grayling. Appendix -Table A.5 shows the decomposition of inertia and chi-square for the four core traits (life form, life span, seed dispersal and pollination mode).

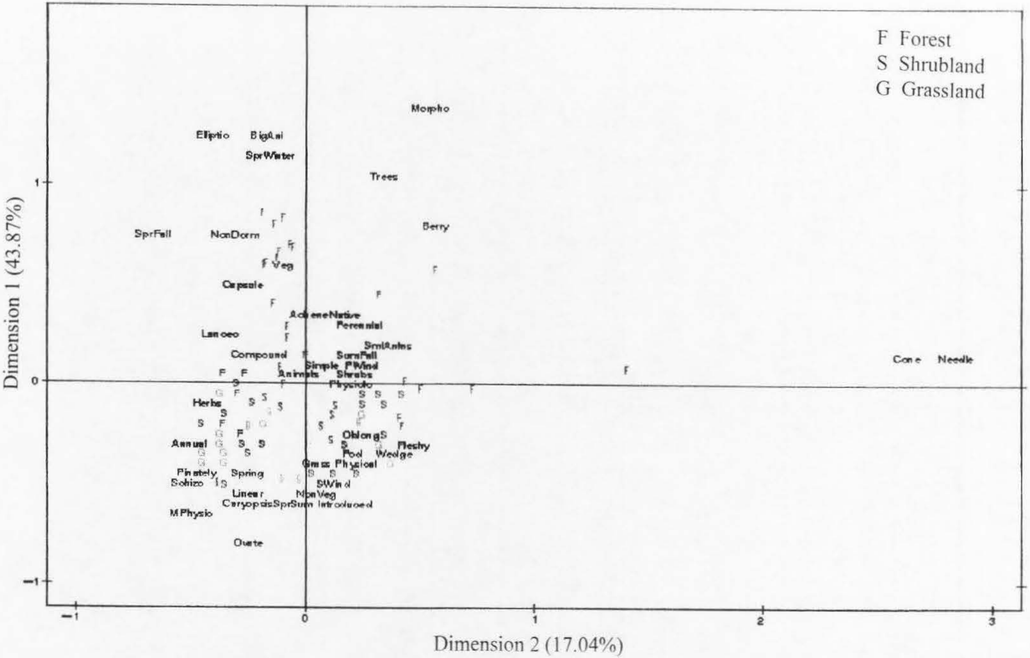


Figure 12. Biplot for correspondance analysis in all qualitative variables for Camp Williams, UT.

Dimension 1 and 2 explain 53% (33 and 20%, respectively) of the association between functional types and traits. The relationship between row and columns is not completely explained by two dimensions; however, to simplify interpretation, only the first two dimensions are illustrated.

The ordination biplot for the four core traits is shown in Figure 13. Along Dimension 1 life form (grasses, shrubs, and trees) contribute most to the ordination of functional types. Seed dispersal (by both small and big animals), life span (annuals), and pollination by animals are the categories most related to grouping of plots. Along Dimension 2 life form (shrubs) and seed dispersal (small animals and insects) are traits mostly influencing the ordination (Appendix -Table A.5).

It is possible to distinguish four broad classes in the biplot. The first is represented by perennial shrubs with seed dispersal by small animals and insects; the second is perennial trees mostly animal pollinated; the third class includes mostly perennial herbs dispersed by small animals and insects; and the fourth class is consists of annual and perennial grasses with wind pollination and seed dispersal.

Similar to the Camp Williams ordination, when all qualitative variables are included, the Camp Grayling ordination becomes less clear. Appendix -Table A.6 shows 17 dimensions to be significant in explaining the relation between row and columns. The first two dimensions explain approximately 45% of the ordination.

Figure 14 and Appendix -Table A.6 show that along Dimension 1, fruit type, leaf shape, life form, period of flowering season and seed dormancy are traits that contribute most to the ordination of functional types. Along Dimension 2, origin, leaf shape, fruit

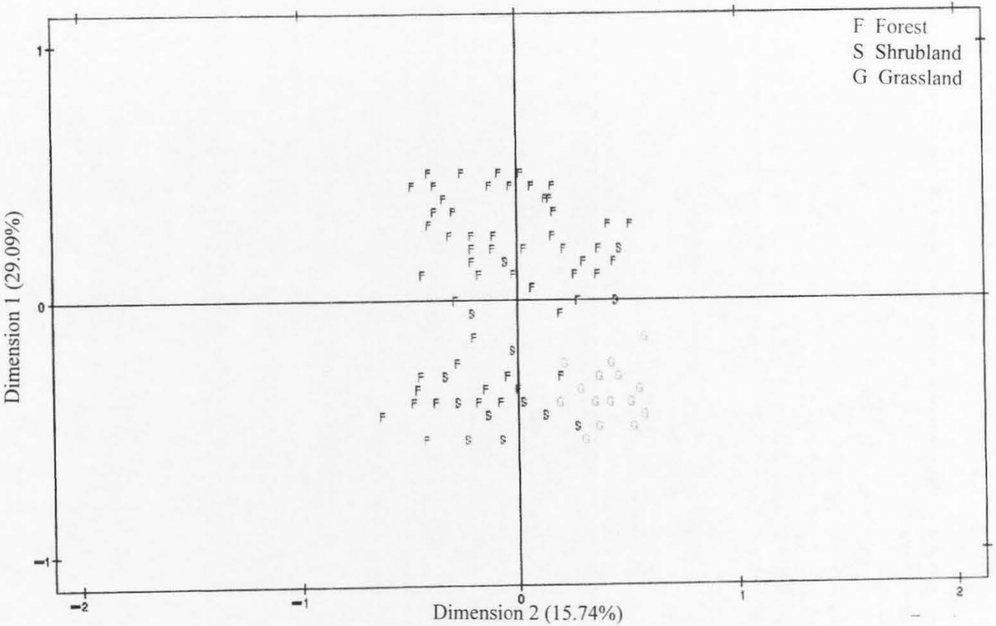


Figure 13. Biplot for correspondance analysis in the "core traits" for Camp Grayling, MI.

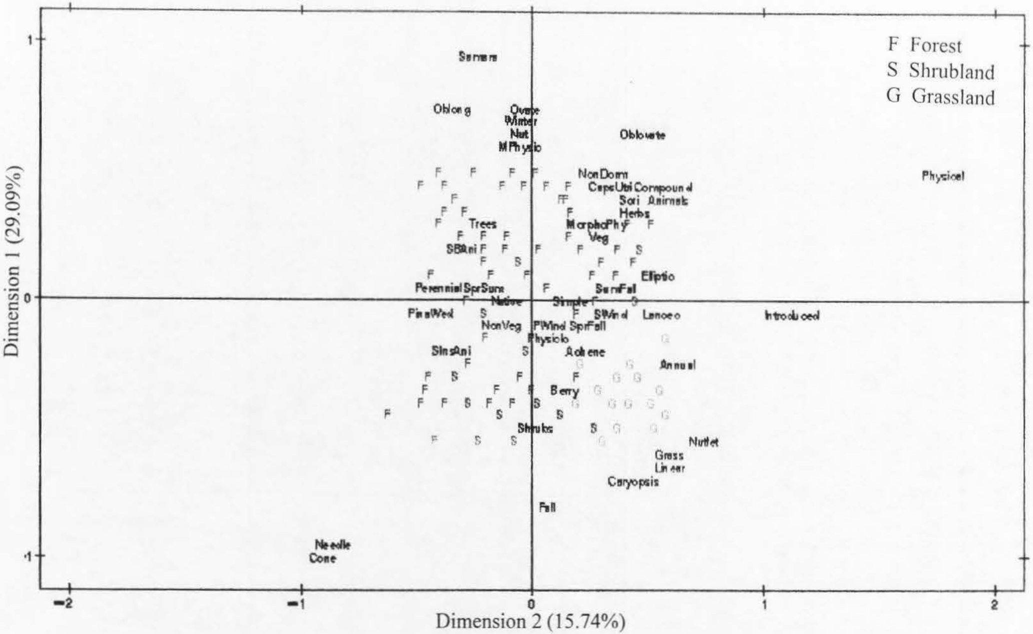


Figure 14. Biplot for correspondance analysis in all qualitative variables for Camp Grayling, MI.

type, seed dormancy and life form are traits that explain most of the inertia and chi-square.

Analysis of both installations with this particular statistical technique (CA) and two different approaches (few versus all traits) show that including a large number of traits and derived classes does not necessarily improve the ordination of functional types. This could be caused by the intrinsic trait variation in functional types (plots); however, it might be that a small number of core traits are sufficient to explain the distribution of traits within and between functional types. Besides the issue of few versus many traits to define "plant communities"/functional types, it is interesting to analyze: (1) if among the traits there is a set that characterizes a functional type; or (2) if there are similar sets of traits that can be identified consistently in different functional types; and (3) if there are trends or patterns in traits within and between functional types?

Correspondence analysis for functional types

Figures 12 and 14 illustrate ordinations using all qualitative variables both for Camp Williams and Camp Grayling. These ordinations assess similarities in the trait structure within and between functional types.

Correspondence analysis ordinates plant communities based on similarity of functional traits. Points in the graph with the same symbols represent grassland, shrubland or forest functional type communities. In general, in both installations the functional types defined most clearly are grassland and forest. Shublands in both installations are intermediate to the other two functional types and sometimes clearly within one or the other. This can be possible because functional groups are defined by the set of functional traits regardless of the species included. Sometimes, functional types cannot be clearly defined because there is high variation in the functional groups. This sort of ambiguity can result even with direct observation of a community; for example, a mostly grass-dominated community with a few big trees might be identified in the field as either a grassland or a woodland. The grassland functional type in Figures 12 and 14 is generally associated with traits such as annuals, introduced, linear leaves, and caryopsis as a fruit. Tree functional types include traits like perennial, native, compound leaves, seed dispersal by small and big animals and insects and pollination by wind.

Assessment of traits between functional types

Tables 6 and 7 include results of the ANOVA for functional types at Camp Williams and Camp Grayling, respectively. Results were used to evaluate expected differences in traits associated with an increase in complexity (i.e., grassland to forest) (A in Figure 15).

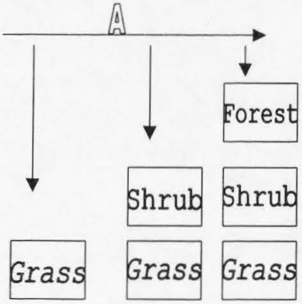


Figure 15. Conceptual model showing the direction and vector used in the analysis.

Table 6. ANOVA results for the different functional types in Camp Williams, UT

Traits	GRASSLAND	SHRUBLAND	FOREST	PR < F
Richness	12.60^{ab}	11.83^{b}	14.35^{a}	0.2883
Shannon Spp	1.82^{a}	1.88^{a}	1.92^{a}	0.6133
Shannon Trait	2.03^{a}	2.06^{a}	1.67^{b}	< .0001
Cover	95.66^{ab}	83.16^{b}	113.42^{a}	0.0018
SeedWind	0.7275^{a}	0.7879^{a}	0.3631^{b}	< .0001
SeedSmAnIns	0.2639^{b}	0.2120^{b}	0.3604^{a}	0.0003
SeedBigAnimls	0.0085^{b}	0.0^{b}	0.2764^{a}	< .0001
Pwind	0.6670^{a}	0.4376^{b}	0.6468^{a}	< .0001
Panimals	0.3329^{b}	0.5623^{a}	0.3531^{b}	< .0001

a, b=Different letters indicate significant differences in mean values.

Table 7. ANOVA results for the different functional types in Camp Grayling, MI

Traits	GRASSLAND	SHRUBLAND	FOREST	PR < F
Richness	10.73^{a}	11.84^{a}	13.29^{a}	0.1330
Shannon Spp	1.74^{a}	1.79^{a}	1.94^{a}	0.0629
Shannon Trait	1.89^{a}	1.95^{a}	1.95^{a}	0.1666
Cover	97.67^{c}	148.92^{b}	186.74^{a}	< .0001
SeedWind	0.6983^{a}	0.4518^{b}	0.4313^{b}	< .0001
SeedSmAnIns	0.1809^{b}	0.3457^{a}	0.3033^{ab}	0.0457
SeedBigAnimls	0.1206^{b}	0.2023^{ab}	0.2653^{a}	0.0074
Pwind	0.8707^{a}	0.8146^{a}	0.8191^{a}	0.3923
Panimals	0.1292^{a}	0.1854^{a}	0.1808^{a}	0.3923

a, b=Different letters indicate significant differences in mean values.

Both species and trait diversity seem to be essentially independent of functional type. There is a significant decrease in trait diversity for the forest function type at Camp Williams, but this is not reflected in the Camp Grayling data. Cover and richness increase for both installations even though the increase in richness is not significant for Camp Grayling. For all of the functional types, richness at Camp Williams is slightly higher than Camp Grayling. It is commonly thought that arid environments with low potential productivity are unable to maintain a high number of species; at least with respect to Camp Williams, this is not true. This may relate at least in part to the frequency of disturbance at Camp Williams that may have promoted a high number of introduced species.

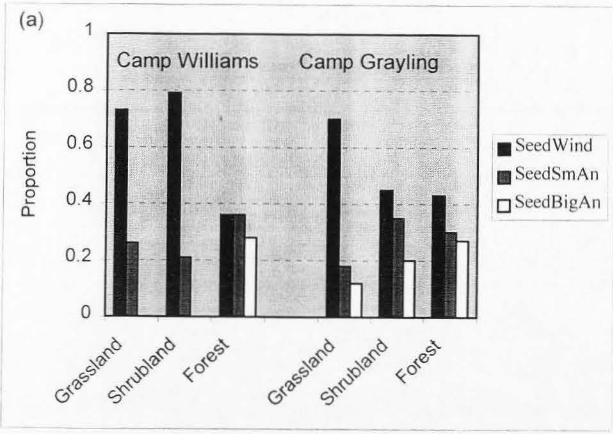
Figure 16 (a) and (b) and Appendix -Tables A.7 and A.8 show the proportions for seed dispersal and pollination mode between functional types for both installations.

A higher proportion of wind seed dispersal is found in less complex functional types at both installations. Camp Grayling has a greater diversity of dispersal agents in contrast to Camp Williams, which only showed a high variety in the most complex communities (forest).

While wind pollination dominates at both installations, there is a substantially higher proportion of wind pollination at Camp Grayling. This might be related to the presence of taller species with natural adaptations to this pollination mode. In contrast, for Camp Williams the proportions for animal pollination are higher and, in general, there are short individuals with large seeds (Appendix -Table A.7 and A.8).

Additional trait comparisons between functional types are presented in Figure 17 for (a) life origin, (b) life span, (c) leaf type and (d) reproductive mode. At Camp Williams, there is a direct relationship between functional type complexity and an increase of natives, perennials, simple leaves and higher proportions of non-vegetative reproduction.

Functional type complexity appears to have less influence at Camp Grayling. Functional types at Camp Grayling are characterized by high proportions of native



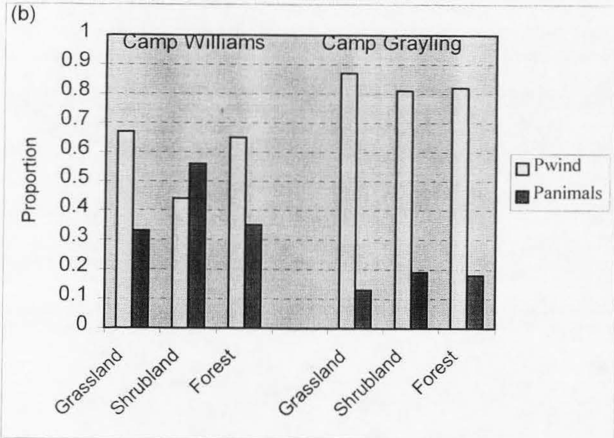


Figure 16. Proportions for seed dispersal (a) and pollination mode (b) by functional types in Camp Williams, UT, and Camp Grayling, MI.

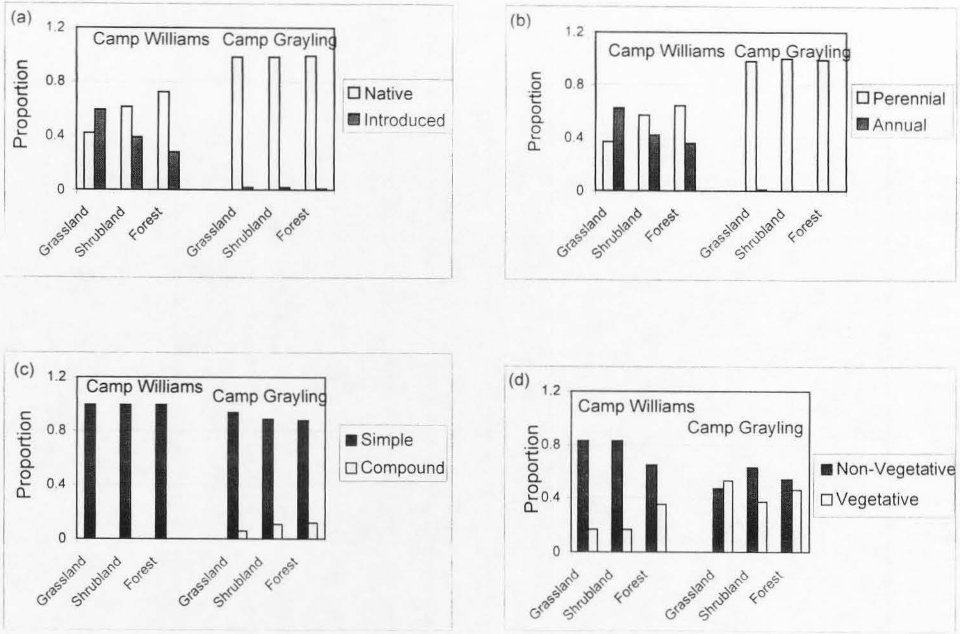


Figure 17. Proportions for origin (a), life span (b), leaf type (c) and reproductive mode (d), respectively for functional types in Cammp Williams, UT and Camp Grayling, MI.

perennials, simple leaves and variable vegetative reproduction. The proportion of compound leaves increases with functional type complexity.

Assessment of traits within functional types

Results represented in Tables 8 and 9 and Appendix -Tables A.9 and A.10 were used to test hypotheses relating to trait patterns from top to bottom within a given functional type (vector B in Figure 18).

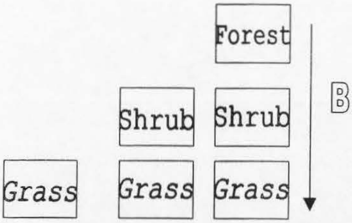


Figure 18. Conceptual model showing the direction and vector used in the analysis.

Overall species and trait diversity, cover, richness and the proportion of seed dispersal by small animals and insects increase from top to bottom within the tree functional type at Camp Williams. In contrast, the proportion of wind pollination and seed dispersal decrease from top to bottom.

For Camp Grayling there is an overall reduction in richness, species and trait diversity index, cover and proportion of seed dispersal by insects and small animals from top to bottom of the functional type. There is also an increase in the proportion of seed dispersal and pollination by wind from top to bottom within the functional type.

Table 8. ANOVA analysis within a functional type in Camp Williams, UT

Traits	TREESgss 31	TREEshr 32	TREEStree 33	PR > F
Richness	10.25^{a}	3.2308^{b}	1.1071^{c}	0.0001
Shannon Spp	1.7925^{a}	0.8341^{b}	0.0683^{c}	< .0001
Shannon Trait	1.9372^{a}	1.4562^{b}	1.4035^{c}	< .0001
Cover	58.893^{a}	17.269^{c}	38.50^{b}	< .0001
SeedWind	0.5070^{b}	0.7714^{a}	0.0^{c}	< .0001
SeedSmAnIns	0.4929^{a}	0.2285^{b}	0.2267^{b}	0.0037
SeedBigAnimls	0.0^{b}	0.0^{b}	0.7732^{a}	< .0001
Pwind	0.5478^{b}	0.0128^{c}	1.0^{a}	< .0001
Panimals	0.4521^{b}	0.9871^{a}	0.0^{c}	< .0001

a, b=Different letters indicate significant differences in mean values.

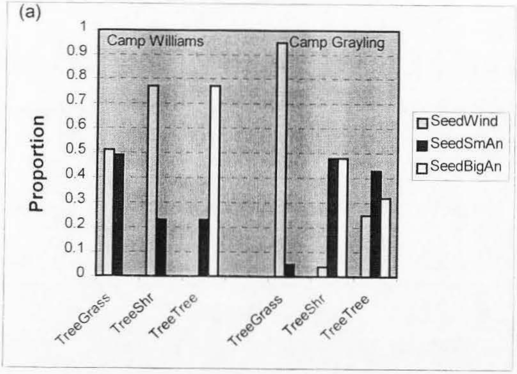
Table 9. ANOVA analysis within a functional type in Camp Grayling, MI

Traits	TREEgss 31	TREEshr 32	TREEStree 33	PR > F
Richness	4.6481^{a}	3.3846^{b}	5.333^{a}	0.0001
Shannon Spp	0.9671^{b}	0.7535^{c}	1.1983^{a}	< .0001
Shannon Trait	1.5772^{b}	1.5744^{b}	1.6396^{a}	0.0173
Cover	48.481^{b}	23.26^{c}	116.44^{a}	< .0001
SeedWind	0.9505^{a}	0.0437^{c}	0.2521^{b}	< .0001
SeedSmAnIns	0.0494^{b}	0.4774^{a}	0.4333^{a}	< .0001
SeedBigAnimals	0.0^{c}	0.4788^{a}	0.3145^{b}	< .0001
Pwind	0.9454^{a}	0.6320^{c}	0.7907^{b}	< .0001
Panimals	0.0545^{c}	0.3679^{a}	0.2092^{b}	< .0001

a, b=Different letters indicate significant differences in mean values.

Contrary to expectations, cover at Camp Williams increases from top to bottom within a functional type. This seems to be related to high species diversity and richness in the bottom functional group.

The overall proportion of seed dispersal by wind increases from top to bottom within the most complex functional type. Since seed dispersal is correlated to seed size, bigger seeds (less prone to be dispersed by wind) are located in the top positions of the functional type (Figure 19 and Appendix -Table A.9 and A.10).



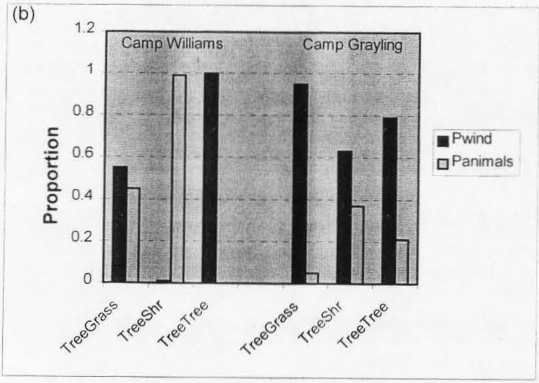


Figure 19. Proportion of (a) seed dispersal and (b) pollination mode within the forest functional type for Camp Williams, UT, and Camp Grayling, MI.

Figure 20 shows the proportions for (a) life span, (b) origin, (c) leaf type and (d) reproductive mode for Camp Williams and Camp Grayling. Functional groups in Camp Williams from top to bottom are characterized by a decrease in the proportion of perennial natives with a high and constant proportion of simple leaves. Contrary to expectations there is an overall increase in non-vegetative reproduction from top to bottom at Camp Williams; however, this is likely the result of very low tree species richness and the fact that one of the species (oak) is vigorous sprouter (i.e., vegetative reproduction).

The pattern in Camp Grayling seems to be less variable between functional groups and is characterized by high proportions of perennial natives with simple leaves and variable reproduction mode. Consistent with expectations, the proportion of compound leaves increases in the bottom layers, except for Camp Williams where there are no compound leaves.

Another striking difference between installations relates to the proportion of annuals in the grass functional type. The relatively high proportion of annuals at Camp Williams may reflect the harsher semi-arid environmental conditions, which could promote species adapted to annual life cycles. In addition, many of these annuals are introduced species with aggressive colonization habits.

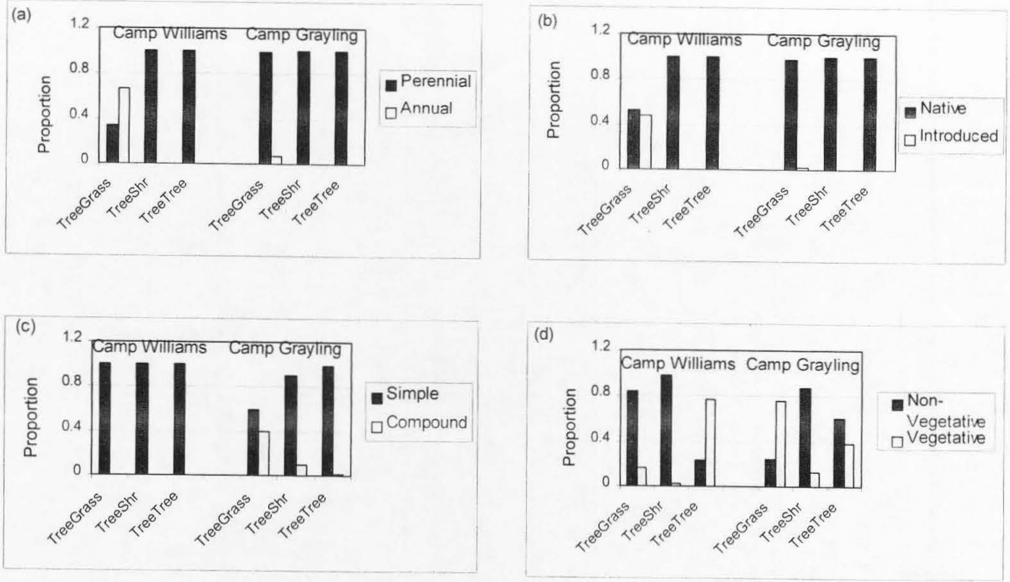


Figure 20. Proportion for (a) life span, (b) origin, (c) leaf type, and (d) reproductive mode for Camp Williams, UT, and Camp Grayling, MI within a functional type.

Assessment of traits across the top of functional types

Tables 10 and 11 (Appendix -Tables A.11 and A.12) have results of the ANOVA of traits for both installations. The comparisons are for differences in traits between the top functional group going from simple to complex functional types (vector C in Figure 21).

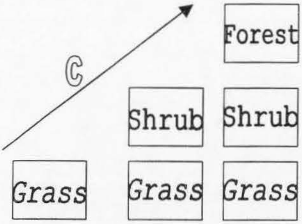


Figure 21. Conceptual model showing the direction and vector used in the analysis.

For Camp Williams there is a reduction in richness, species and trait diversity and cover in the top functional groups from simple to complex functional types. Contrary to the expectations, mean cover for the top functional group decreases with increasing functional type complexity. High values for species diversity and richness could be related to this particular pattern. The proportion of wind seed dispersal shows an overall increase from the grass to the forest functional type. This pattern is reversed for wind pollination.

For Camp Grayling there is an overall increase in cover, species and trait diversity index and a decrease in richness from simple to complex functional types in the top

Table 10. ANOVA results for top functional groups in Camp Williams, UT

Traits	GSSgss 11	SHRshr 22	TREEtree 33	PR > F
Richness	9.8^{a}	2.875^{b}	1.1071^{c}	< .0001
Shannon Spp	1.57^{a}	0.6739^{b}	0.0683^{c}	< .0001
Shannon Trait	1.9551^{a}	1.3902^{b}	1.4035^{b}	< .0001
Cover	83.667^{a}	25.667^{c}	38.50^{c}	< .0001
SeedWind	0.7011^{b}	0.9904^{a}	0.0^{c}	< .0001
SeedSmAnIns	0.2988^{a}	0.0095^{b}	0.2267^{a}	0.0025
SeedBigAnimls	0.0^{b}	0.0^{b}	0.7732^{a}	< .0001
Pwind	0.7362^{b}	0.0007^{c}	1.0^{a}	< .0001
Panimals	0.2637^{b}	0.9992^{a}	0.0^{c}	< .0001

a, b=Different letters indicate significant differences in mean values.

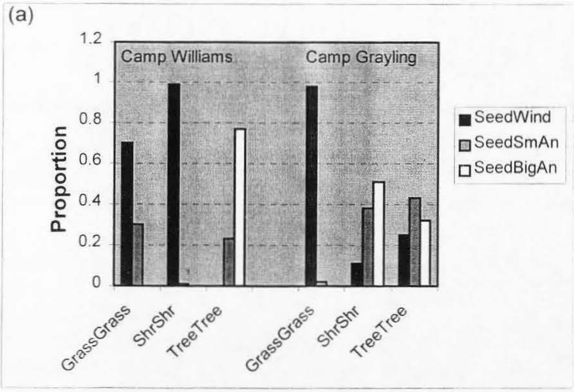
Table 11. ANOVA results for top functional groups in Camp Grayling, MI

Traits	GSSgss 11	SHRshr 22	TREEtree 33	PR > F
Richness	6.071^{a}	4.1538^{b}	5.333^{ab}	0.0624
Shannon Spp	1.1733^{a}	0.8302^{b}	1.1983^{a}	0.0092
Shannon Trait	1.1482^{b}	1.1632^{a}	1.6396^{a}	< .0001
Cover	71.43^{b}	52.08^{c}	116.44^{a}	< .0001
SeedWind	0.9779^{a}	0.1120^{c}	0.2521^{b}	< .0001
SeedSmAnIns	0.0220^{b}	0.3783^{a}	0.4333^{a}	0.0002
SeedBigAnimls	0.0^{c}	0.5097^{a}	0.3145^{b}	< .0001
Pwind	0.9521^{a}	0.6969^{b}	0.7907^{b}	0.0007
Panimals	0.0478^{b}	0.3030^{a}	0.2092^{a}	0.0007

a, b=Different letters indicate significant differences in mean values.

functional groups. Contrary to the expectations, the proportion of wind pollination and seed dispersal decrease from simple to complex functional types (Figure 22).

It seems that trees for both installations commonly have big seeds that are dispersed by animals. Animal pollination is important at both installations; for example, at Camp Williams animals pollinate almost 100% of the shrub species.



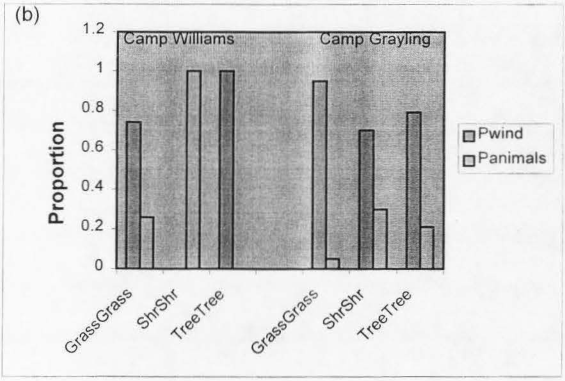


Figure 22. Proportion of seed dispersal (a) and pollination mode (b) for top functional groups in Camp Williams, UT, and Camp Grayling, MI.

Figure 23 (a), (b), (c), and (d) show the proportions for origin, life span, leaf type and reproductive mode for Camp Williams and Camp Grayling. Annuals and native species are dominant in the grass functional group at Camp Williams and are almost absent in the same functional group in Camp Grayling. Compound leaves are absent from Camp Williams. There is no clear pattern with respect to reproduction mode for either installation.

Assessment of traits across the bottom of functional types

The final group of comparisons related to the internal structure of plant communities examines the lower functional group from simple to complex functional types (vector D in Figure 24).

Tables 12 and 13 include the ANOVA results for Camp Williams and Camp Grayling. Figure 25 and Appendix -Tables A.13 and A.14 were used to assess this gradient.

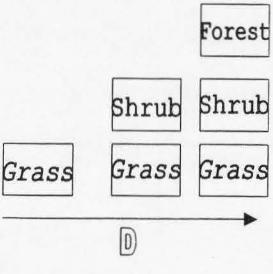


Figure 24. Conceptual model showing the direction and vector used in the analysis.

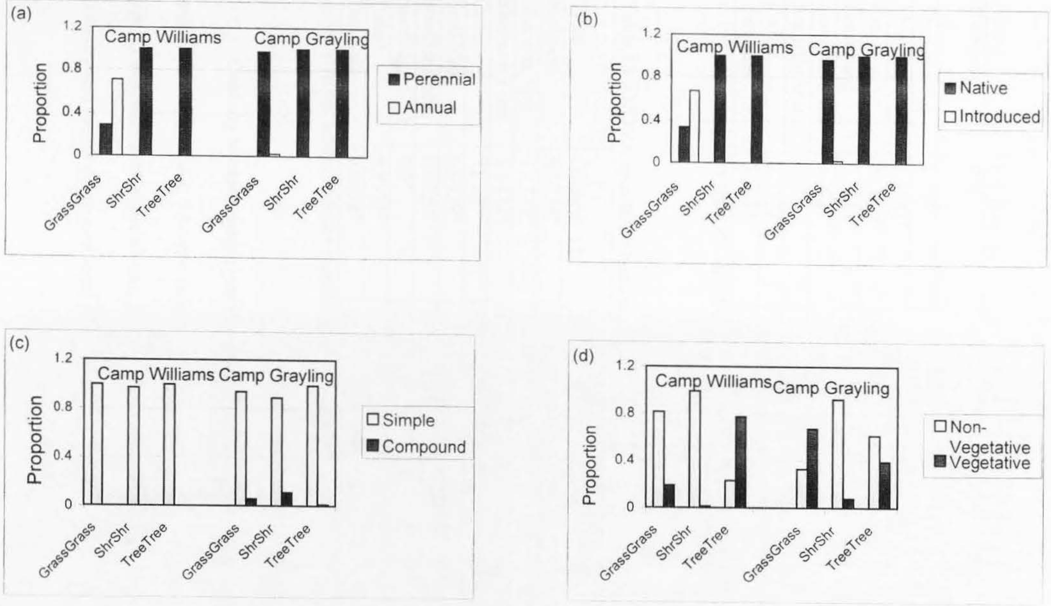


Figure 23. Proportion for (a) life span, (b) origin, (c) leaf type, and (d) reproductive mode for Camp Williams, UT and Camp Grayling, MI across top functional types..

Table 12. ANOVA results for bottom functional groups in Camp Williams, UT

Traits	GSSgss 11	SHRUBgss 21	TREESgss 31	PR > F
Richness	9.8^{a}	8.83^{a}	10.25^{a}	0.2547
Shannon Spp	1.57^{a}	1.577^{a}	1.7925^{a}	0.0602
Shannon Trait	1.9551^{a}	1.9706^{a}	1.9372^{a}	0.3974
Cover	83.667^{a}	57.25^{b}	58.89^{b}	0.0100
SeedWind	0.7011^{a}	0.6931^{a}	0.5070^{b}	0.0013
SeedSmAnIns	0.2988^{b}	0.3068^{b}	0.4929^{a}	0.0013
SeedBigAnimls	0.0^{a}	0.0^{a}	0.0^{a}	--
Pwind	0.7362^{a}	0.6383^{ab}	0.5478^{b}	0.0064
Panimals	0.2637^{b}	0.3616^{ab}	0.4521^{a}	0.0064

a, b=Different letters indicate significant differences in mean values.

Table 13 ANOVA results for bottom functional groups in Camp Grayling, MI

Traits	GSSgss 11	SHRUBgss 21	TREESgss 31	PR > F
Richness	6.0714^{a}	6.0^{a}	4.6481^{a}	0.0788
Shannon Spp	1.1733^{a}	1.1164^{a}	0.9672^{a}	0.2151
Shannon Trait	1.1482^{b}	1.5130^{a}	1.5772^{a}	<.0001
Cover	71.42^{a}	66.18^{a}	48.48^{b}	0.0044
SeedWind	0.9779^{a}	0.9738^{a}	0.9505^{a}	0.7184
SeedSmAnIns	0.0220^{a}	0.0261^{a}	0.0494^{a}	0.7184
SeedBigAnimls	0.0^{a}	0.0^{a}	0.0^{a}	--
Pwind	0.9521^{a}	0.9632^{a}	0.9454^{a}	0.9129
Panimals	0.0478^{a}	0.0367^{a}	0.0545^{a}	0.9128

a, b=Different letters indicate significant differences in mean values.

Contrary to expectations, for Camp Williams there is an increase in richness and species diversity within the same functional group from simple to complex functional types. Consistent with expectations, there are decreases in richness, species diversity, trait diversity and the proportion of wind pollination and seed dispersal.

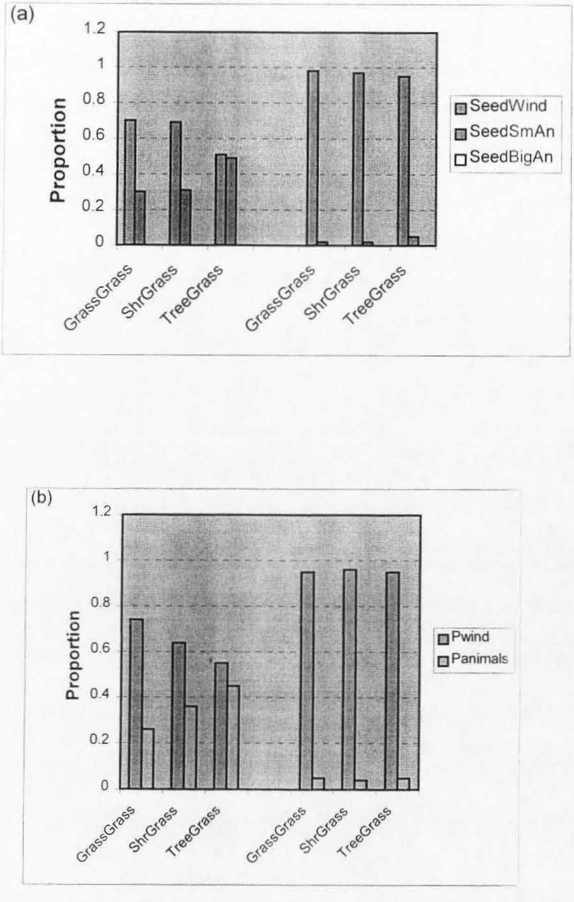


Figure 25. Proportion of (a) seed dispersal and (b) pollination mode for grass functional groups from simple to complex functional types Camp Williams, UT, and Camp Grayling, MI.

Also consistent with expectations, there are increases in species diversity, cover and the proportion of wind pollination and seed dispersal for Camp Grayling. Contrary to expectations, there is an increase in trait diversity for the lower functional group from simple to complex functional types.

Figure 26 presents the graphic for (a) life form, (b) origin, (c) leaf type, and (d) reproduction mode. In general, and regardless of the functional type, the low functional groups at Camp Williams can be characterized by a set of traits that include high proportions of introduced annuals, simple linear leaves and predominantly non-vegetative reproduction.

With respect to Camp Grayling, there is a somewhat different set of functional traits for lower functional groups. High proportions of perennial native individuals with simple leaves and vegetative reproduction mode characterize this group. The proportion of compound leaves increases in the lower functional group when another functional group is above.

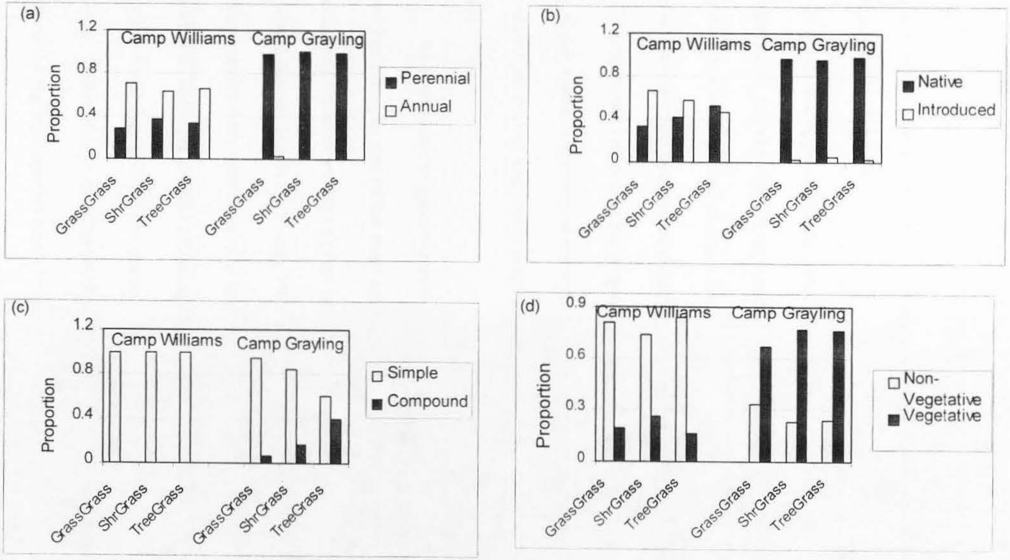


Figure 26. Proportions for (a) life span, (b) origin, (c) leaf type, and (d) reproductive mode for Camp Williams, UT, and Camp Grayling, MI, across the bottom of functional types.

CHAPTER 7

DISCUSSION

The conceptual model

A traditional approach to the description of plant community structure has been based on species. A criticism of this approach is that a broad characterization of vegetation response to environmental changes cannot just rely on phylogeny because most plant species have limited geographic distributions. Thus global, or even regional, scale predictions based on species are geographically constrained. On the other hand, even at fine scales characterizations of community structure based on species may mask important patterns of vegetation response and processes (Pillar 1999; McIntyre et al. 1999).

An alternative to species-based community characterizations is based on plant traits. For example, one of the most common approaches used is to seek consistent associations between groups of plant traits and environmental conditions, independent of the actual species involved (Keddy 1992). According to Orloci (1991), "character-based" implies species free, with taxonomy merely implicit in the particular traits being considered. There are several advantages of using these sorts of "character-based" classifications: they provide the opportunity to compare and predict responses, for example, to disturbance of different floras or even the behavior of a species not currently a part of the regional species pool (Wilson et al. 1994); they describe the structure and functioning of ecosystems (Orloci 1991; Diaz et al. 1999); they also may provide insight into the mechanisms underlying vegetation response (McIntyre et al. 1999); and they may be useful in summarizing biodiversity in natural systems (Diaz et al. 1999).

A functional trait can be any plant characteristic that may have adaptive or strategic "functional significance" (Lavorel et al. 1999b). Functional groups are made up of broad sets of functional traits and are analogous to guilds in animal communities or strata in traditional species-based plant community classifications. Plant functional types, made up of one to several functional groups, are analogous to species-based vegetation types. The use of plant functional traits, groups and types implies that a direct or indirect relationship between traits, community and ecosystem processes is present. Similarly, at the level of an individual species, it is presumed possible to associate a particular set of traits with that species' place in community structure and dynamics.

The conceptual model used to describe the vertical structure of communities is based on life forms (Figures 2 and 3). Life forms are commonly used descriptors in plant community ecology and often are associated with important traits such as plant size (Lavorel et al. 1999b); life forms are also assumed to capture many of the individual's functions in the ecosystem. In particular, life form classifications have been related to disturbance effects and ecosystem processes. Life forms are a simple way to account for variation identifying vegetation or traits only comparable at finer levels of detail (McIntyre et al. 1999).

The model has three different functional types (Grassland, Shrubland, and Forest functional types) formed by one to three functional groups (Grass, Shrub, and Tree functional group). Functional types, analogous to community or vegetation type, are defined by the relative abundance of life forms. A functional group on the other hand, is made up of those species within the functional type having similar life form.

The model is a general, simple and practical framework for the analysis of the internal structure of plant communities based on functional traits. It provides a framework for detailed analysis of the functional characteristics between and within functional types.

The use of functional traits provides better *a priori* knowledge about the characteristics, structure and function of the ecosystem under study (McIntyre et al. 1999). In particular, the conceptual model allowed a broad description of and insight into the communities present, for example, under mesic versus drier conditions. The conceptual model facilitated characterization of the general types of species present in those communities. Even when environmental conditions are not explicitly included, it is possible to explore possible relationships between environmental factors and community structure. In the future, environmental factors could be incorporated into the model.

The broad definition of functional groups could be an advantage or disadvantage depending on the particular objectives. The conceptual model does provide a general description of the functional groups and their associated traits. However, a more detailed analysis of the internal structure of communities will likely require a more specific and numerous list of functional traits (Semenova & van der Maarel 2000). Nevertheless, this classification approach, based on groups of a relative few key traits, proved to be a useful method to organize the hierarchical structure of plant communities.

Functional traits and groups

There are consistent sets of functional traits associated with the different functional groups. In addition, there are regular patterns of traits among the functional groups. For example, the grass functional group, characterized by annual and perennial herbs and grasses, has both pollination and seed dispersal generally dominated by wind and a relatively short spring and summer flowering period. The shrub functional group, dominated by native perennials, has seed dispersal by both wind and low mobility insects and animals; similarly, pollination is by both wind and animals. The flowering period is intermediate in length between the other two functional groups. Finally, native perennials form the tree functional group that has great diversity of seed dispersal mechanisms (wind, low and high mobility insects and animals), pollination predominately by wind and a flowering period lasting throughout the growing season.

There are traits that are not associated with any particular functional group and are therefore of no help in characterizing or differentiating between functional groups. For example, physiological seed dormancy is present in high proportions in all of the functional groups and functional types.

Conceptually, the functional groups and their characteristic traits can be used to "construct" or "assemble" a plant community. For example, a community of the shrub functional type has an understory with characteristics associated with the grass functional group and an overstory with traits consistent with the shrub functional group. Adding or subtracting functional groups and their associated traits can at least in a broad sense characterize a community.

Community structure

Figure 10 shows the four categories of hypotheses tested; these are in the context of Functional Trait patterns and comparisons within and between Functional Types and Functional Groups. Functional types are characterized by the dominant life forms from Grassland, Shrub to Forest and this classification is comparable to a species-based vegetation type. Functional groups integrate the same life forms. For example, in a forest functional type there is a functional group in which the dominant life forms are the trees, another one with shrubs and a third group consisting of mainly grasses.

Differences between functional types, the fairly simple grass type to the more complex forest type, are represented by vector A (Figure 10). Comparisons from top to bottom within a functional type are represented by the vector B. Comparisons within the same functional group across different functional types are indicated by vector D. Finally, comparisons between the top functional groups across functional types are represented by the vector C.

As expected, cover increases with increasing complexity of functional type; however, this is one of few community-level variables strongly associated with functional type. In contrast, richness, species diversity and trait diversity are largely independent of functional type complexity. This counter-intuitive result suggests, for example, that the diversity of plant functional traits for plant communities is fairly consistent regardless of climatic regime or structural complexity. These results are consistent with Pillar's (1999) observation that even phylogentically distant communities may be similar with respect to plant traits.

While many variables do not present clear trends when data from both sites are pooled, some patterns emerge when the analysis is done separately for each installation. In contrast to Camp Grayling, at Camp Williams there is a predominance of introduced annuals with simple leaves, pollination and seed dispersal by wind and mostly non-vegetative reproduction.

Overall values for richness and species diversity, while not always significantly different, appear to be at least somewhat higher for Camp Williams. According with Rey-Benayas (1995), climate strongly influences community richness. For example, while extremely arid environments may have low species diversity due to unfavorable conditions for germination and establishment of all but a few highly specialized species, semi-arid ecosystems such Camp Williams may have higher species diversity than more mesic ecosystems, at least in North America (Cornelius et al. 1991). Steep environmental gradients and small-scale heterogeneity associated with changes in elevation, slope, aspect and soils at Camp Williams might also contribute to slightly greater species diversity and richness (Vivian-Smith 1997).

Camp Williams also has had a greater exposure to chronic disturbances, such as wildfires and grazing by domestic livestock, than Camp Grayling. It seems likely that this disturbance regime may also contribute to higher proportions of introduced species (Wilson 1989b). This is consistent with observations that the majority of plants colonizing recently disturbed areas at Camp Williams are non-native. Increase in introduced species is thought to be directly related to declines in abundance of native species, apparently not just in Camp Williams but in western rangelands as replacement of longer lived perennial grasses and herbs by shorter-lived annual species is taking place (INRMP 2001).

It is generally thought that introduced species cannot successfully invade undisturbed sites occupied by native species with high richness. Both in absolute and relative terms, Camp Grayling has low numbers of introduced species. The communities of this installation have high proportions of native perennials. Vegetative and non-vegetative reproduction are about equally represented. While seed dispersal is predominately by wind, seed dispersal by animals is better represented than in the plant communities at Camp Williams. Pollination is predominantly by wind at Camp Grayling, and pollination by animals is significantly lower than for Camp Williams.

Simple leaves predominate at both installations; however, unlike Camp Williams, at Camp Grayling compound leaves are present. It is assumed that the presence of compound leaves results from more mesic conditions at Camp Grayling. This trait has been associated with understory conditions of low light and high moisture (Pausas 1994), and there is, in fact, a clear increase in the proportion of compound leaves from grassland to forest functional types. The higher percentages of perennial species at Camp Graying are also consistent with the observation by Henry & Aarssen (1997) that plants under low irradiance are characterized by increased longevity.

Modes of pollination and seed dispersal are two of the more important aspects of life histories in vascular plants (Feinsinger 1987; Feinsinger et al. 1987). Animal associations confer more efficient and effective pollination and dispersal than wind (Kelly 1996). Interestingly, Camp Williams has a higher proportion of animal pollination than Camp Grayling but a lower proportion of seed dispersal by animals.

Tall forests are generally dominated by seeders (Kruger et al. 1997), and this is reflected in the high proportion of non-vegetative reproduction for Camp Grayling. One somewhat surprising result was the high proportion of vegetative reproduction in the tree functional type at Camp Williams. The expected increase in the proportion of vegetative reproduction from top to bottom of complex functional types is also reflected in the results, with the exception, again, of the tree functional type at Camp Williams. The tree functional group at Camp Williams essentially consists of only two tree species and one of these, gamble oak, is an extremely effective sprouter.

There are sets of traits that define functional groups within communities (Figure 10, vector B). While there are not strong generalizations apparent across the two installations, it is possible to distinguish patterns of internal structure within the functional types of a given installation.

For example, at Camp Williams, richness, species diversity, cover, trait diversity, seed dispersal by wind and pollination by animals all show a significant increase between functional groups from the top to bottom of a functional type. These patterns apparently result from the extremely simple tree functional group at Camp Williams.

Disturbance, in the form of livestock grazing and fire, seems to have played an important role in shaping plant communities at Camp Williams. Chronic disturbance could change community composition by perturbing soil and water processes, altering resource availability and plant competition (McIntyre et al. 1999). This in turn can influence the relative proportion of species present and their collective functional traits. For example, bottom functional groups are dominated by annual introduced species with simple leaves, which are strongly associated with disturbances such as grazing and frequent fire regimes (McIntyre et al. 1999; INRMP 1999). In particular, high values of richness, cover, species, and trait diversity seem to be correlated; many species in the grass functional group increases trait diversity and dramatically increases cover.

Plant communities at Camp Grayling have decreases in richness, cover, species and trait diversity index as functional groups change from top to bottom within a functional type. Substantially greater cover in the tree functional group, in contrast with Camps Williams, certainly results in a substantial different understory environment with less light that may limit species richness and trait diversity. While the lowest functional group is less diverse, overall functional type diversity is greater for Camp Grayling's plant communities; this may result from substantially more productive sites.

There are similar sets of functional traits for the same functional groups in different functional types (Figure 10, vector D). Independent of the functional type it is in, the grass functional group has about the same richness, cover, species diversity, trait diversity and proportions of seed dispersal and pollination by wind. In contrast, functional type is associated with grass functional group cover. At both installations, there is a significant reduction in grass functional group cover from simple to complex functional types presumably as a result of the space occupied by species in the shrub and tree functional groups. For Camp Grayling plant communities, there is a significant, but slight, increase in trait diversity within the grass group from simple to complex functional types. With this exception the structure of the grass functional group is remarkably similar independent of functional type or installation. Richness, species diversity, trait diversity, wind pollination and seed dispersal are essentially the same. The consistency between installations is particularly striking given the fundamental taxonomic differences between the grass functional group at Camp Williams and at Camp Grayling. At Camp Williams the grass functional group is dominated by introduced annuals with simple leaves; at Camp Grayling it is dominated by native perennials with compound leaves.

There are patterns in the characteristics of functional groups located at the tops of different functional types (Figure 10, vector C). For several characteristics, e.g., richness, species diversity, cover, pollination mode, and seed dispersal, there are differences between patterns for the two installations. Patterns in trait diversity, on the other hand, are similar.

For Camp Williams plant communities there are significant reductions in richness and cover, as well as species and trait diversity for the top functional group with increasing functional type complexity. For Camp Grayling plant communities, there are no clear patterns for most of the functional traits. In sharp contrast to Camp Williams, cover and richness both increase for the top functional group from simple to complex functional types.

Assembly rules

There are essentially two different ways in which assembly rules are considered. The first, having to do with assembly in the sense of "to build," deals with the sequence in which species are incorporated into a community. In this sense, assembly rules would, for example, dictate whether the presence of species A facilitates or inhibits the subsequent introduction of species B.

The current conceptual model is an example of the second way in which assembly rules are considered. In this view, the internal structure of the community, i.e., the way in which it is assembled, is assumed to reflect interactions or ecological restrictions between species (Wilson 1999). In this approach, internal structure is characterized by functional traits.

Consistent patterns and trends for key functional traits provide support for the view that assembly rules may account for the internal structure of plant communities. Similarity in the sets of functional traits characterizing functional groups in taxonomically dissimilar plant communities suggest that these traits are related to the ecological processes that shape these communities.

Applying this conceptualization to community dynamics, it is possible that entry of a new species into an established community is strongly influenced by the set of functional traits already present. Depending on the situation, entry of the new species could contribute to the assembly of the functional group or perhaps be blocked by an already "complete" functional group. The idea that community development might be predictable relates to the Clementsian deterministic view in which sets of traits are seen as emergent properties that shape communities. Clearly, there is a great deal of overlap between the "sequencing" and "internal structure" views of assembly rules.

In general, assembly rules based on plant characters, as opposed to species, are considered more interesting (Wilson 1999) and may also be more robust. This research in fact found sets of functional traits that appear to characterize structurally similar plant communities from different regions and with completely different species compositions. It is, however, important to consider that the data base comes from two very contrasting environments, and there are clear differences between the two installations. Some of the ambiguity in results might be explained if the analysis of functional traits were extended to data from additional installations; this would, for example, allow replication of the contrasting climatic conditions represented by Camp Williams and Camp Grayling.

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APPENDIX

Table A.1. Example of the AERCOV file in 1995 for Camp Williams, UT.

PLOTID[1]	VEGLOC[2]	VEGHT[3]	VEGID[4]
1	0.50	0.00	G
1	1.50	0.00	L
1	1.50	0.10	ARTR
1	1.50	0.20	ARTR
1	1.50	0.40	ARTR
1	1.50	0.40	PUTR
1	1.50	0.50	PUTR
1	2.50	0.00	L
1	2.50	0.30	ARTR
1	2.50	0.40	ARTR
1	2.50	0.70	ARTR
1	3.50	0.00	L
1	3.50	0.20	ARTR
1	4.50	0.00	L
1	4.50	0.80	ARTR
1	5.50	0.00	R
1	5.50	0.10	ALAL
1	6.50	0.00	BG
1	7.50	0.00	L
1	7.50	0.20	BRTE
1	7.50	0.80	PUTR
1	8.50	0.00	L
1	8.50	0.10	BRTE
1	8.50	0.30	ARTR
1	9.50	0.00	L
1	9.50	0.60	ARTR
1	9.50	0.70	ARTR
1	9.50	0.90	ARTR
1	10.50	0.00	L
1	10.50	0.50	ARTR
1	10.50	0.60	ARTR
1	10.50	0.70	ARTR
1	10.50	0.80	ARTR
1	10.50	0.90	ARTR
1	10.50	1.00	ARTR
1	10.50	1.10	ARTR
1	10.50	1.20	ARTR
1	11.50	0.00	L
1	11.50	0.40	ARTR
1	11.50	0.60	ARTR
1	11.50	0.70	ARTR
1	11.50	0.80	ARTR
1	12.50	0.00	R
1	13.50	0.00	BG
1	13.50	0.20	GUSA
1	14.50	0.00	L
1	14.50	0.50	PUTR

(1) Plot identification (1/100), (2) Vegetation location along line transect, (3) Vegetation height, (4) Vegetation identification.

Table A.2. Example of the Floristic data base (Plant list) for Camp Williams, UT

PLOTID	VEGID	FAMILY	GENUS	SPEC	LIFE	ORIGIN	FORM1	COMMONNAME
WILL	ACMI	ASTERACEAE	Achillea	millefolium	perennial	Native	herb	Yarrow
WILL	AGCR	POACEAE	Agropyron	cristatum	perennial	Introduce	graminoid	Created wheatgrass
WILL	AGGL	ASTERACEAE	Agoseris	glauca	perennial	Native	herb	Mountain dandelion
WILL	ALAC	LILIACEAE	Allium	acuminatum	perennial	Native	herb	Tapertip onion
WILL	ALAL	BRASSICACEAE	Alyssum	alyssoides	annual	Introduce	herb	Yellow alyssum
WILL	AMAL	AMARANTHACEAE	Amaranthus	albus	annual	Native	herb	Tumbling pigweed
WILL	AMAL1	ROSACEAE	Amelanchier	alnifolia	perennial	Native	shrub	Serviceberry
WILL	AMPS	ASTERACEAE	Ambrosia	psilostachya	perennial	Native	herb	Western ragweed
WILL	ARAR	ASTERACEAE	Artemisia	arbuscula	perennial	Native	shrub	Low sagebrush
WILL	ARLU	ASTERACEAE	Artemisia	ludoviciana	perennial	Native	herb	Foothill sage
WILL	ARMI	ASTERACEAE	Arctium	minus	biennial	Introduce	herb	Small burdock
WILL	ARTH	BRASSICACEAE	Arabidopsis	thaliana	annual	Introduce	herb	Mouse-ear cress
WILL	ARTR	ASTERACEAE	Artemisia	tridentata	perennial	Native	shrub	Big sagebrush
WILL	ASBE	FABACEAE	Astragalus	beckwithii	perennial	Native	herb	Beckwith milkvetch
WILL	ASCH	ASTERACEA	Aster	chilensis	perennial	Native	herb	Wasatch fleabane
WILL	ASCO	FABACEAE	Astragalus	convallarius	perennial	Native	herb	Timber milkvetch
WILL	BASA	ASTERACEAE	Balsamorhiza	sagittata	perennial	Native	herb	Arrowleaf balsamroot
WILL	BERE	BERBERIDACEAE	Berberis	repens	perennial	Native	shrub	Oregon grape
WILL	BRCA1	ASTERACEAE	Brickellia	californica	perennial	Native	shrub	California brickellbush
WILL	BRCA	POACEAE	Bromus	carinatus	perennial	Native	graminoid	Mountain brome
WILL	BRJA	POACEAE	Bromus	japonicus	annual	Introduce	graminoid	Japanese chess
WILL	BRMI	ASTERACEAE	Brickellia	microphyllla	perennial	Native	shrub	LittleleafBrickellbush
WILL	BRTE	POACEAE	Bromus	tectorum	annual	Introduce	graminoid	Cheatgras
WILL	CAGE	CYPERACEAE	Carex	geyeri	perennial	Native	graminoid	Elk sedge
WILL	CANU1	ASTERACEAE	Carduus	nutans	annual	Introduce	herb	Nodding musk thistle
WILL	CANU	LILIACEAE	Calochortus	nuttallii	perennial	Native	herb	Sego lily
WILL	CEMA1	ASTERACEAE	Centaurea	maculosa	biennial	Introduce	herb	Spotted knapweed
WILL	CEMA	RHAMNACEAE	Ceanothus	martinii	perennial	Native	herb	Utah mountain lilac
WILL	CEMO	ROSACEAE	Cercocarpus	montanus	perennial	Native	shrub	Alderleafmountain
WILL	CHNA	ASTERACEA	Chrysothamnus	nauseosus	perennial	Native	shrub	Rubber rabbitbrush
WILL	CHVI	ASTERACEA	Chrysothamnus	viscidiflorus	perennial	Native	shrub	Green Rabbitbrush

Table A.3. Correspondance Analysis for "core traits" in Camp Williams, UT

```
                           Inertia and Chi-Square Decomposition

Singular    Principal       Chi-                  Cumulative
   Value      Inertia     Square     Percent         Percent    11   22   33   44   55
                                                                ----+---+---+---+---+--
 0.38988      0.15200    4017.14       56.27           56.27    **************************
 0.25266      0.06383    1687.03       23.63           79.90    ***********
 0.15049      0.02265     598.53        8.38           88.28    ****
 0.12323      0.01519     401.34        5.62           93.90    ***
 0.09655      0.00932     246.38        3.45           97.35    **
 0.07763      0.00603     159.27        2.23           99.59    *
 0.03347      0.00112      29.60        0.41          100.00

   Total      0.27014    7139.29      100.00

Degrees of Freedom = 660

                                     Row Coordinates

                                                     Dim1       Dim2

                          Annual                  -0.3613    -0.2233
                          Perennial                0.3016     0.1864
                          Grass                   -0.3568    -0.1711
                          Herbs                   -0.1788    -0.1011
                          Shrubs                   0.0100     0.7555
                          Trees                    1.0951    -0.2735
                          SWind                   -0.4252     0.0559
                          Insects                  0.4851     0.1079
                          SmallA                   0.6038    -0.2082
                          PWind                    0.0389    -0.2152
                          Animals                 -0.0563     0.3119
```

Continued on next page

Table A.3. Correspondance Analysis for "core traits" in Camp Williams, UT

Summary Statistics for the Row Points

	Quality	Mass	Inertia
Annual	0.8835	0.1137	0.0860
Perennial	0.8835	0.1363	0.0718
Grass	0.8043	0.0989	0.0712
Herbs	0.2569	0.0630	0.0383
Shrubs	0.9321	0.0460	0.1044
Trees	0.9461	0.0421	0.2098
SWind	0.9207	0.1413	0.1045
Insects	0.4442	0.0466	0.0958
SmallA	0.7156	0.0621	0.1310
PWind	0.7359	0.1479	0.0356
Animals	0.7359	0.1021	0.0516

Partial Contributions to Inertia for the Row Points

	Dim1	Dim2
Annual	0.0977	0.0889
Perennial	0.0815	0.0742
Grass	0.0828	0.0453
Herbs	0.0133	0.0101
Shrubs	0.0000	0.4118
Trees	0.3320	0.0493
SWind	0.1681	0.0069
Insects	0.0721	0.0085
SmallA	0.1489	0.0422
PWind	0.0015	0.1073
Animals	0.0021	0.1555

Table A.4. Correspondance Analysis for all qualitative variables in Camp Williams, UT

```
                     Inertia and Chi-Square Decomposition
Singular   Principal     Chi-                 Cumulative
  Value     Inertia     Square    Percent      Percent       9   18   27   36   45
                                                         ----+---+---+---+---+--
0.37936    0.14391    10459.1      43.87        43.87    ************************
0.24057    0.05788     4206.2      17.64        61.52    **********
0.20564    0.04229     3073.5      12.89        74.41    *******
0.15508    0.02405     1748.0       7.33        81.74    ****
0.10519    0.01107      804.2       3.37        85.12    **
0.09040    0.00817      594.0       2.49        87.61    *
0.08202    0.00673      488.9       2.05        89.66    *
0.08062    0.00650      472.3       1.98        91.64    *
0.06629    0.00439      319.3       1.34        92.98    *
0.06148    0.00378      274.7       1.15        94.13    *
0.05823    0.00339      246.4       1.03        95.17    *
0.05284    0.00279      202.9       0.85        96.02
0.05002    0.00250      181.9       0.76        96.78
0.04653    0.00216      157.3       0.66        97.44
0.03947    0.00156      113.2       0.47        97.92
0.03546    0.00126       91.4       0.38        98.30
0.03226    0.00104       75.6       0.32        98.62
0.03149    0.00099       72.1       0.30        98.92
0.02842    0.00081       58.7       0.25        99.16
0.02796    0.00078       56.8       0.24        99.40
0.02454    0.00060       43.8       0.18        99.59
0.01895    0.00036       26.1       0.11        99.70
0.01622    0.00026       19.1       0.08        99.78
0.01469    0.00022       15.7       0.07        99.84
0.01448    0.00021       15.2       0.06        99.91
0.01210    0.00015       10.6       0.04        99.95
0.00841    0.00007        5.1       0.02        99.97
0.00718    0.00005        3.7       0.02        99.99
0.00514    0.00003        1.9       0.01       100.00
Degrees of Freedom = 2772
```

Continued on next page

Table A.4. Correspondance Analysis for all qualitative variables in Camp Williams, UT

```
                         Inertia and Chi-Square Decomposition

   Singular   Principal      Chi-               Cumulative
      Value     Inertia    Square    Percent       Percent      9   18   27   36   45
                                                              ----+----+----+----+----+--
    0.00371     0.00001       1.0       0.00        100.00
      Total     0.32801   23838.9     100.00

   Degrees of Freedom = 2772
                                        Row Coordinates

                                                   Dim1          Dim2

                         Annual                 -0.3642       -0.1242
                         Perennial               0.3040        0.1037
                         Grass                  -0.3791       -0.0545
                         Herbs                  -0.1345       -0.1622
                         Shrubs                  0.0476        0.1007
                         Trees                   1.0401        0.2607
                         SWind                  -0.4028       -0.0478
                         SmlAnIns                0.1944        0.2208
                         BigAni                  1.2307       -0.2780
                         PWind                   0.0179        0.0241
                         Animals                -0.0259       -0.0349
                         Native                  0.3079        0.0716
                         Introduced             -0.4748       -0.1104
                         Simple                  0.0000       -0.0002
                         Compound               -0.0022        0.0633
                         Elliptic                1.2505       -0.2888
                         Needle                  0.1658        2.7325
                         Fleshy                 -0.1857        0.2286
                         Lanceo                  0.2682       -0.2450
                         Linear                 -0.3090       -0.0973
```

Continued on next page

Table A.4. Correspondance Analysis for all qualitative variables in Camp Williams, UT

Row Coordinates

	Dim1	Dim2
Oblong	-0.2397	0.1141
Ovate	-0.7758	-0.3439
Pinately	-0.4723	-0.3381
Wedge	-0.3432	0.2630
Achene	0.3674	-0.0927
Berry	0.7858	0.4728
Capsule	0.4884	-0.4114
Caryopsis	-0.4023	-0.0492
Cone	0.1658	2.7325
Pod	-0.3541	0.1349
Schizo	-0.4958	-0.3893
NonDorm	0.7637	-0.4471
Morpho	1.3904	0.4279
Physical	-0.4743	-0.0335
Physiolo	-0.0371	0.0419
MPhysio	-0.6260	-0.6170
NonVeg	-0.2066	0.0641
Veg	0.6040	-0.1874
SprFall	0.7571	-0.5556
SprSum	-0.2278	-0.0597
SumFall	0.1411	0.1023
Spring	-0.4924	-0.2525
SprWinter	1.1335	-0.3115

Table A.5. Correspondance Analysis for "core traits" in Camp Grayling, MI

```
                         Inertia and Chi-Square Decomposition

 Singular   Principal      Chi-                Cumulative
   Value     Inertia     Square    Percent       Percent        7   14   21   28   35
                                                              ----+---+---+---+---+--
 0.27807     0.07732     4172.0     33.63         33.63     ************************
 0.21972     0.04828     2604.7     20.99         54.62     ***************
 0.19460     0.03787     2043.4     16.47         71.09     ************
 0.18423     0.03394     1831.4     14.76         85.85     ***********
 0.12120     0.01469      792.5      6.39         92.24     *****
 0.10270     0.01055      569.1      4.59         96.83     ***
 0.08540     0.00729      393.5      3.17        100.00     **

   Total     0.22994    12406.6    100.00

Degrees of Freedom = 820


                                 Row Coordinates

                                         Dim1         Dim2

                   Perennial          -0.0008       0.0007
                   Annual              0.3648      -0.3135
                   Grass               0.7411      -0.3844
                   Herbs              -0.1455      -0.0959
                   Shrubs              0.4683       0.4954
                   Trees              -0.4197       0.0271
                   SWind               0.0578      -0.2322
                   Insects             0.2107       0.5147
                   SmallA             -0.3746      -0.1770
                   PWind               0.0563      -0.0472
                   Animals            -0.2625       0.2199
```

Continued on next page

Table A.5. Correspondance Analysis for "core traits" in Camp Grayling, MI

Summary Statistics for the Row Points

	Quality	Mass	Inertia
Perennial	0.0154	0.2494	0.0001
Annual	0.0154	0.0006	0.0363
Grass	0.9343	0.0536	0.1740
Herbs	0.0447	0.0270	0.0797
Shrubs	0.5482	0.0397	0.1465
Trees	0.8227	0.1297	0.1212
SWind	0.4813	0.1173	0.0607
Insects	0.7491	0.0733	0.1317
SmallA	0.3581	0.0593	0.1237
PWind	0.2169	0.2059	0.0223
Animals	0.2169	0.0441	0.1038

Partial Contributions to Inertia for the Row Points

	Dim1	Dim2
Perennial	0.0000	0.0000
Annual	0.0010	0.0011
Grass	0.3809	0.1641
Herbs	0.0074	0.0051
Shrubs	0.1127	0.2020
Trees	0.2954	0.0020
SWind	0.0051	0.1310
Insects	0.0421	0.4024
SmallA	0.1077	0.0385
PWind	0.0084	0.0095

Table A.6. Correspondance Analysis for all qualitative variables in Camp Grayling, MI.

```
                          Inertia and Chi-Square Decomposition
  Singular   Principal      Chi-                Cumulative
     Value     Inertia    Square    Percent        Percent     6   12   18   24   30
                                                             ----+---+---+---+---+-
   0.33245     0.11052   16269.1      29.09          29.09   ************************
   0.24457     0.05982    8804.9      15.74          44.83   *************
   0.23253     0.05407    7959.0      14.23          59.06   ************
   0.19248     0.03705    5453.3       9.75          68.81   ********
   0.16462     0.02710    3988.9       7.13          75.94   ******
   0.12578     0.01582    2328.9       4.16          80.11   ***
   0.11929     0.01423    2094.6       3.75          83.85   ***
   0.10134     0.01027    1511.9       2.70          86.56   **
   0.08962     0.00803    1182.3       2.11          88.67   **
   0.08388     0.00704    1035.6       1.85          90.52   **
   0.07998     0.00640     941.7       1.68          92.21   *
   0.07139     0.00510     750.3       1.34          93.55   *
   0.06573     0.00432     635.9       1.14          94.68   *
   0.06089     0.00371     545.7       0.98          95.66   *
   0.05727     0.00328     482.8       0.86          96.52   *
   0.05314     0.00282     415.6       0.74          97.27   *
   0.05043     0.00254     374.4       0.67          97.94   *
   0.04043     0.00163     240.6       0.43          98.37
   0.03839     0.00147     216.9       0.39          98.75
   0.03317     0.00110     162.0       0.29          99.04
   0.03098     0.00096     141.3       0.25          99.30
   0.02837     0.00081     118.5       0.21          99.51
   0.02227     0.00050      73.0       0.13          99.64
   0.02168     0.00047      69.2       0.12          99.76
   0.01679     0.00028      41.5       0.07          99.84
   0.01563     0.00024      36.0       0.06          99.90
   0.01348     0.00018      26.8       0.05          99.95
   0.00978     0.00010      14.1       0.03          99.97
   0.00734     0.00005       7.9       0.01          99.99
  Degrees of Freedom = 3483
```

Continued on next page

Table A.6. Correspondance Analysis for all qualitative variables in Camp Grayling, MI.

```
                       Inertia and Chi-Square Decomposition
 Singular   Principal    Chi-                Cumulative
   Value     Inertia    Square    Percent      Percent     6   12   18   24   30
                                                        ----+----+----+----+----+--
 0.00556     0.00003       4.6       0.01      100.00
 0.00292     0.00001       1.3       0.00      100.00
 0.00212     0.00000       0.7       0.00      100.00
 0.00141     0.00000       0.3       0.00      100.00

   Total     0.37995   55929.6     100.00

 Degrees of Freedom = 3483

                                     Row Coordinates

                                               Dim1         Dim2

                          Perennial          0.0006      -0.0012
                          Annual            -0.2528       0.5317
                          Grass             -0.6168       0.4974
                          Herbs              0.3347       0.3586
                          Shrubs            -0.4498       0.0276
                          Trees              0.3246      -0.2905
                          SWind              0.0710       0.1829
                          SInsAni           -0.2226      -0.2176
                          SBAni              0.1368      -0.0944
                          PWind             -0.0802      -0.0254
                          Animals            0.3738       0.1184
                          Native             0.0004      -0.0099
                          Introduced        -0.0360       0.9655
                          Simple            -0.0556      -0.0456
                          Compound           0.4078       0.3344
                          Elliptic           0.1496       0.0539
                          Needle            -0.9573      -0.9851
```

Continued on next page

Table A.6. Correspondance Analysis for all qualitative variables in Camp Grayling, MI.

Row Coordinates		
	Dim1	Dim2
Lanceo	-0.0627	0.4597
Linear	-0.6317	0.4933
Oblong	0.7403	-0.2183
Ovate	0.7517	-0.1189
Oblovate	0.6555	0.3430
PinaWed	-0.0621	-0.2976
Achene	-0.1822	0.1161
Berry	-0.4183	0.1513
CapsUtri	0.4177	0.1043
Caryopsis	-0.7207	0.2988
Cone	-0.9845	-1.0112
Nut	0.6345	-0.1160
Nutlet	-0.5496	0.6397
Samara	0.9521	-0.3414
Sori	0.3847	0.3602
NonDorm	0.5103	0.1767
MorphoPhy	0.3121	0.1219
Physical	0.4807	1.6540
Physiolo	-0.1384	-0.0454
MPhysio	0.5797	-0.1664
NonVeg	-0.1076	-0.2445
Veg	0.1251	0.2841
SprFall	0.0124	0.0665
SprSum	0.0728	-0.0670
SumFall	0.0286	0.2450
Fall	-0.8062	0.0068
Winter	0.6771	-0.1621

Table A.7. ANOVA results for assessment of traits between functional types in Camp Williams, UT

Trait-Class	GSS	SHRUB	WOODS	PR < F
MaxTotHt	3.85^{b}	2.41^{c}	8.92^{a}	< .0001
MaxVeght	0.76^{b}	0.75^{b}	1.28^{a}	0.0186
Leaf Size	7.37^{a}	6.88^{a}	8.11^{a}	0.2012
Seed Size	5.26^{a}	5.57^{a}	6.05^{a}	0.2461
Perennials	0.3762^{b}	0.5780^{a}	0.6405^{a}	< .0001
Annuals	0.6237^{a}	0.4219^{b}	0.3594^{b}	< .0001
Native	0.4146^{c}	0.6110^{b}	0.7230^{a}	< .0001
Introduced	0.5853^{a}	0.3889^{b}	0.2769^{c}	< .0001
Simple	0.9975^{a}	0.9957^{a}	0.9988^{a}	0.3024
Compound	0.0024^{a}	0.0042^{a}	0.0011^{a}	0.3024
Elliptic	0.0330^{b}	0.0124^{b}	0.3540^{a}	< .0001
Needle	0.0090^{b}	0.0036^{b}	0.0717^{a}	0.0171
Fleshy	0.0028^{a}	0.0022^{a}	0.0023^{a}	0.9464
Lanceolated	0.010^{a}	0.0082^{a}	0.0163^{a}	0.4660
Linear	0.7230^{a}	0.5217^{b}	0.3867^{c}	< .0001
Oblong	0.0961^{b}	0.1415^{a}	0.0794^{b}	0.0086
Ovate	0.0096^{a}	0.0051^{ab}	0.0004^{b}	0.0024
Pinately	0.062^{a}	0.0378^{a}	0.0340^{a}	0.1772
Wedge	0.0537^{b}	0.2671^{a}	0.0549^{b}	< .0001
Achene	0.1997^{b}	0.4158^{a}	0.4189^{a}	< .0001
Berry	0.0028^{a}	0.0032^{a}	0.0085^{a}	0.1996
Capsule	0.0976^{a}	0.0423^{b}	0.1356^{a}	0.0016
Caryopsis	0.5867^{a}	0.3890^{b}	0.2857^{c}	< .0001
Cone	0.0090^{b}	0.0036^{b}	0.0717^{a}	0.0171
Pod	0.0979^{ab}	0.1420^{a}	0.0783^{b}	0.0099
Schizocarp	0.0060^{a}	0.0038^{a}	0.0011^{a}	0.1081
Non-Dormant	0.0371^{ab}	0.0303^{b}	0.0746^{a}	0.0481
Morphological	0.0012^{b}	0.0^{b}	0.0113^{a}	0.0062
Physical	0.0007^{a}	0.0^{a}	0.0^{a}	0.1779
Physiological	0.9010^{a}	0.9527^{a}	0.9046^{a}	0.0675
MorphoPhyisio	0.0597^{a}	0.0169^{b}	0.0094^{b}	0.0013
Non Vegetative	0.8284^{a}	0.8341^{a}	0.6511^{b}	< .0001
Vegetative	0.1715^{b}	0.1658^{b}	0.3488^{a}	< .0001
SpringFall	0.0369^{a}	0.0123^{a}	0.0545^{a}	0.0781
SpringSummer	0.5380^{a}	0.4285^{b}	0.3827^{b}	0.0012
SummerFall	0.4158^{b}	0.5526^{a}	0.5578^{a}	0.0031
Spring	0.0091^{a}	0.0055^{a}	0.0040^{a}	0.5809
SpringWinter	0.0^{a}	0.0008^{a}	0.0008^{a}	0.5809

Table A.8. ANOVA results to assess traits between functional types in Camp Grayling, MI

Trait-Class	GSS	SHRUB	TREES	PR < F
MaxTotHt	24.067^{c}	29.077^{b}	38.148^{a}	< .0001
MaxVeght	2.71^{c}	4.8198^{b}	7.5595^{a}	< .0001
Leaf Size	12.32^{ab}	10.97^{b}	12.659^{a}	0.0532
Seed Size	4.1568^{b}	4.9887^{b}	6.681^{a}	< .0001
Perennials	0.9845^{b}	1.0^{a}	0.998^{a}	0.0295
Annuals	0.015^{a}	0.0	0.0019^{b}	0.0295
Native	0.9781^{a}	0.9811^{a}	0.9938^{a}	0.0773
Introduced	0.0218^{a}	0.0188^{a}	0.0061^{a}	0.0773
Simple	0.9406^{a}	0.8901^{a}	0.8793^{a}	0.1236
Compound	0.0593^{a}	0.1098^{a}	0.1206^{a}	0.1236
Elliptic	0.1798^{b}	0.34906^{a}	0.3662^{a}	0.0056
Needle	0.0103^{b}	0.1842^{a}	0.1210^{a}	0.0172
Lanceolated	0.0511^{a}	0.0423^{a}	0.0309^{a}	0.4625
Linear	0.6742^{a}	0.3188^{b}	0.1524^{c}	< .0001
Oblong	0.0159^{a}	0.0084^{a}	0.0338^{a}	0.1229
Ovate	0.0684^{b}	0.0929^{b}	0.2905^{a}	< .0001
Oblovate	0.0^{a}	0.0033^{a}	0.0034^{a}	0.7017
PinatelyWedge	0.0^{a}	0.0007^{a}	0.0004^{a}	0.6908
Achene	0.0108^{a}	0.0019^{a}	0.0051^{a}	0.4081
Berry	0.2303^{b}	0.3199^{a}	0.1365^{c}	< .0001
CapsuleUtricule	0.0302^{a}	0.0869^{a}	0.1026^{a}	0.1131
Caryopsis	0.2457^{a}	0.1267^{b}	0.0541^{c}	< .0001
Cone	0.0103^{b}	0.1842^{a}	0.1177^{ab}	0.0183
Nut	0.022^{b}	0.0223^{b}	0.2153^{a}	< .0001
Nutlet	0.4079^{a}	0.1633^{b}	0.0861^{c}	< .0001
Samara	0.0^{b}	0.0273^{b}	0.1823^{a}	< .0001
Sori	0.0424^{a}	0.0671^{a}	0.1000^{a}	0.0644
Non-Dormant	0.0686^{b}	0.1210^{b}	0.2212^{a}	0.0018
MorphoPhysical	0.0^{a}	0.0^{a}	0.0016^{a}	0.6631
Physical	0.0^{b}	0.0017^{a}	0.0^{b}	0.0688
Physiological	0.9313^{a}	0.8752^{a}	0.7698^{b}	0.0014
MorphoPhyisio	0.0^{a}	0.0018^{a}	0.0072^{a}	0.2740
Non Vegetative	0.4710^{b}	0.6308^{a}	0.5379^{ab}	0.1010
Vegetative	0.5289^{a}	0.3691^{b}	0.4620^{ab}	0.1010
SpringFall	0.0404^{a}	0.0199^{a}	0.0395^{a}	0.5079
SpringSummer	0.6040^{b}	0.5692^{b}	0.7073^{a}	0.0002
SummerFall	0.2064^{a}	0.1777^{a}	0.1729^{a}	0.5725
Fall	0.1484^{b}	0.2120^{a}	0.0573^{c}	< .0001
Winter	0.0006^{a}	0.0209^{a}	0.0228^{a}	0.2096

Table A.9. ANOVA results for assessment of traits within functional types in Camp Williams, UT

Trait-Class	TREESgss 31	TREEshr 32	TREEStree 33	PR > F
MaxTotHt	1.80^{c}	2.6920^{b}	8.928^{a}	< .0001
MaxVeght	0.4184^{b}	0.5628^{b}	1.2439^{a}	< .0001
Leaf Size	8.399^{b}	5.561^{c}	13.23^{a}	< .0001
Seed Size	5.777^{b}	3.7933^{c}	14.75^{a}	< .0001
Perennials	0.3444^{b}	1.0^{a}	1.0^{a}	< .0001
Annuals	0.6555^{a}	0.0^{b}	0.0^{b}	< .0001
Native	0.5251^{b}	1.0^{a}	1.0^{a}	< .0001
Introduced	0.4748^{a}	0.0^{b}	0.0^{b}	< .0001
Simple	0.9980^{a}	0.9989^{a}	1.0^{a}	0.4250
Compound	0.0019^{a}	0.0010^{a}	0.0^{a}	0.4250
Elliptic	0.0663^{b}	0.2101^{b}	0.7732^{a}	< .0001
Needle	0.0^{b}	0.0^{b}	0.2267^{a}	0.0003
Fleshy	0.0^{b}	0.0173^{a}	0.0^{b}	0.0007
Lanceolated	0.0433^{a}	0.0258^{a}	0.0^{a}	0.1937
Linear	0.6959^{a}	0.1793^{b}	0.0^{c}	< .0001
Oblong	0.1368^{a}	0.0445^{b}	0.0^{c}	< .0001
Ovate	0.0007^{a}	0.0^{a}	0.0^{a}	0.3860
Pinately	0.0568^{a}	0.0^{b}	0.0^{b}	< .0001
Wedge	0.0^{b}	0.5226^{a}	0.0^{b}	< .0001
Achene	0.1302^{b}	0.7896^{a}	0.7732^{a}	< .0001
Berry	0.0^{b}	0.0444^{a}	0.0^{b}	< .0001
Capsule	0.1968^{a}	0.1659^{a}	0.0^{b}	0.0004
Caryopsis	0.5190^{a}	0.0^{b}	0.0^{b}	< .0001
Cone	0.0^{b}	0.0^{b}	0.2267^{a}	0.0003
Pod	0.1516^{a}	0.0^{b}	0.0^{b}	< .0001
Schizocarp	0.0021^{a}	0.0^{a}	0.0^{a}	0.1795
Non-Dormant	0.0590^{b}	0.1659^{a}	0.0^{b}	0.0031
MorphoPhysical	0.0137^{ab}	0.0260^{a}	0.0^{b}	0.0731
Physical	0.0^{a}	0.0^{a}	0.0^{a}	--
Physiological	0.9122^{a}	0.8080^{b}	1.0^{a}	0.0012
MorphoPhyisio	0.0143^{a}	0.0^{b}	0.0^{b}	0.0052
Non Vegetative	0.8444^{b}	0.9816^{a}	0.2267^{c}	< .0001
Vegetative	0.1555^{b}	0.0183^{c}	0.7732^{a}	< .0001
SpringFall	0.0157^{b}	0.1659^{a}	0.0^{b}	0.0009
SpringSummer	0.7349^{a}	0.0706^{b}	0.0^{c}	< .0001
SummerFall	0.2400^{c}	0.7634^{b}	1.0^{a}	< .0001
Spring	0.0067^{a}	0.0^{b}	0.0^{b}	0.0189
SpringWinter	0.0025^{a}	0.0^{a}	0.0^{a}	0.2261

Table A.10. ANOVA results to assess traits within functional types in Camp Grayling, MI

Trait-Class	TREEgss 31	TREEshr 32	TREEStree 33	PR > F
MaxTotHt	1.55^{b}	2.567^{b}	38.14^{a}	< .0001
MaxVeght	0.555^{b}	0.6437^{b}	7.559^{a}	< .0001
Leaf Size	16.4389^{a}	7.193^{c}	12.4737^{b}	< .0001
Seed Size	1.9894^{c}	4.7713^{b}	11.5698^{a}	< .0001
Perennials	0.9930^{b}	1.0^{a}	1.0^{a}	< .0001
Annuals	0.0069^{a}	0.0^{b}	0.0069^{b}	< .0001
Native	0.9783^{b}	1.0^{a}	1.0^{a}	0.0003
Introduced	0.0216^{a}	0.0^{b}	0.0^{b}	0.0003
Simple	0.5977^{c}	0.8989^{b}	0.9922^{a}	< .0001
Compound	0.4022^{a}	0.1010^{b}	0.0077^{c}	< .0001
Elliptic	0.3889^{b}	0.6448^{a}	0.2925^{b}	< .0001
Needle	0.0^{b}	0.0^{b}	0.2250^{a}	< .0001
Lanceolated	0.0019^{b}	0.0080^{b}	0.0527^{a}	< .0001
Linear	0.5709^{a}	0.0558^{b}	0.0^{c}	< .0001
Oblong	0.0^{b}	0.0746^{a}	0.0375^{ab}	0.0094
Ovate	0.0373^{c}	0.1972^{b}	0.3919^{a}	< .0001
Oblovate	0.0^{a}	0.0^{a}	0.0171^{a}	0.0799
PinatelyWedge	0.0^{a}	0.0012^{a}	0.0^{a}	0.1878
Achene	0.0206^{a}	0.0^{b}	0.0^{b}	0.0236
Berry	0.0149^{b}	0.8931^{a}	0.058^{b}	< .0001
CapsuleUtricule	0.0072^{b}	0.0346^{b}	0.1636^{a}	< .0001
Caryopsis	0.2365^{a}	0.0^{b}	0.0^{b}	< .0001
Cone	0.0^{b}	0.0^{b}	0.2180^{a}	< .0001
Nut	0.0^{b}	0.055^{b}	0.3178^{a}	< .0001
Nutlet	0.3332^{a}	0.0^{b}	0.0^{b}	< .0001
Samara	0.0^{a}	0.0167^{b}	0.2415^{a}	< .0001
Sori	0.3874^{a}	0.0^{b}	0.0^{b}	< .0001
Non-Dormant	0.3695^{a}	0.1873^{b}	0.0793^{c}	< .0001
MorphoPhysical	0.0014^{a}	0.0^{a}	0.0027^{a}	0.5199
Physical	0.0^{a}	0.0^{a}	0.0^{a}	--
Physiological	0.6094^{b}	0.83^{a}	0.8090^{a}	< .0001
MorphoPhyisio	0.0196^{b}	0.0906^{a}	0.0008^{b}	0.0089
Non Vegetative	0.2378^{c}	0.8665^{a}	0.6065^{b}	< .0001
Vegetative	0.7622^{a}	0.1334^{c}	0.3934^{b}	< .0001
SpringFall	0.0249^{ab}	0.0^{b}	0.0502^{a}	0.0016
SpringSummer	0.4308^{b}	0.2278^{c}	0.9078^{a}	< .0001
SummerFall	0.5386^{a}	0.2766^{b}	0.0190^{c}	< .0001
Fall	0.0042^{b}	0.4223^{a}	0.0^{b}	< .0001
Winter	0.0013^{b}	0.0722^{a}	0.0228^{b}	0.0001

Table A.11. ANOVA results for assessment of traits across top functional types in Camp Williams, UT

Trait-Class	GSSgss 11	SHRUBgss 21	TREESgss 31	PR > F
MaxTotHt	2.093^{a}	1.5104^{b}	1.80^{ab}	0.0892
MaxVeght	0.3265^{a}	0.3732^{a}	0.4184^{a}	0 .4824
Leaf Size	7.645^{a}	7.324^{a}	8.399^{a}	0.4914
Seed Size	5.6769^{a}	6.5012^{a}	5.777^{a}	0.3047
Perennials	0.2895^{a}	0.3701^{a}	0.3444^{a}	0.4374
Annuals	0.7105^{a}	0.6298^{a}	0.6555^{a}	0.4374
Native	0.3347^{b}	0.4180^{ab}	0.5251^{a}	0.0176
Introduced	0.6652^{a}	0.5819^{ab}	0.4748^{b}	0.0176
Simple	0.9971^{a}	0.9926^{a}	0.9980^{a}	0.3917
Compound	0.0028^{a}	0.0073^{a}	0.0019^{a}	0.3917
Elliptic	0.0287^{a}	0.0199^{a}	0.0663^{a}	0.0651
Needle	0.0^{a}	0.0^{a}	0.0^{a}	--
Fleshy	0.0^{a}	0.0^{a}	0.0^{a}	--
Lanceolated	0.0105^{a}	0.0080^{a}	0.0433^{a}	0.3137
Linear	0.7669^{a}	0.6716^{a}	0.6959^{a}	0.2280
Oblong	0.1155^{b}	0.2282^{a}	0.1368^{b}	0.0051
Ovate	0.0102^{a}	0.0077^{a}	0.0007^{b}	0.0093
Pinately	0.0679^{a}	0.0644^{a}	0.0568^{a}	0.8935
Wedge	0.0^{a}	0.0^{a}	0.0^{a}	--
Achene	0.0953^{a}	0.1167^{a}	0.1302^{a}	0.7818
Berry	0.0^{a}	0.0^{a}	0.0^{a}	--
Capsule	0.1101^{b}	0.0615^{b}	0.1968^{a}	0.0002
Caryopsis	0.6695^{a}	0.5822^{ab}	0.5190^{b}	0.0368
Cone	0.0^{a}	0.0^{a}	0.0^{a}	--
Pod	0.1180^{b}	0.2335^{a}	0.1516^{a}	0.0079
Schizocarp	0.0069^{a}	0.0059^{a}	0.0021^{a}	0.3146
Non-Dormant	0.0432^{a}	0.0450^{a}	0.0590^{a}	0.5326
MorphoPhysical	0.0016^{b}	0.0^{b}	0.0137^{a}	0.0179
Physical	0.0009^{a}	0.0^{a}	0.0^{a}	0.1779
Physiological	0.8887^{a}	0.9293^{a}	0.9122^{a}	0.2892
MorphoPhyisio	0.0654^{a}	0.0256^{b}	0.0143^{b}	0.0100
Non Vegetative	0.8152^{ab}	0.7414^{b}	0.8444^{a}	0.0351
Vegetative	0.1847^{ab}	0.2585^{a}	0.1555^{b}	0.0351
SpringFall	0.0394^{a}	0.0163^{a}	0.0157^{a}	0.1330
SpringSummer	0.6135^{b}	0.6651^{ab}	0.7349^{a}	0.0221
SummerFall	0.3364^{a}	0.3092^{ab}	0.2400^{b}	0.0614
Spring	0.0105^{a}	0.0079^{a}	0.0067^{a}	0.8223
SpringWinter	0.0^{a}	0.0012^{a}	0.0025^{a}	0.5623

Table A.12. ANOVA results to assess traits across the top functional types in Camp Grayling, MI

Trait-Class	GSSgss 11	SHRshr 22	TREEtree 33	PR > F
MaxTotHt	1.325^{b}	2.769^{b}	38.14^{a}	< .0001
MaxVeght	0.3073^{b}	0.5414^{b}	7.559^{a}	< .0001
Leaf Size	14.9680^{a}	6.8738^{c}	12.4737^{b}	< .0001
Seed Size	2.052^{c}	4.638^{b}	11.57^{a}	< .0001
Perennials	0.9772^{b}	1.0^{a}	1.0^{a}	0.0068
Annuals	0.0227^{b}	0.0^{a}	0.0^{a}	0.0068
Native	0.9664^{b}	1.0^{a}	1.0^{a}	< .0001
Introduced	0.0336^{a}	0.0^{b}	0.0^{b}	< .0001
Simple	0.9374^{ab}	0.8934^{b}	0.9922^{a}	0.0105
Compound	0.0626^{ab}	0.1065^{a}	0.0077^{b}	0.0105
Elliptic	0.0781^{c}	0.6352^{a}	0.2925^{b}	< .0001
Needle	0.0^{b}	0.0^{b}	0.2250^{a}	0.0047
Lanceolated	0.0^{b}	0.0123^{ab}	0.0527^{a}	0.0321
Linear	0.8942^{a}	0.1190^{b}	0.0^{c}	< .0001
Oblong	0.0010^{a}	0.0367^{a}	0.0375^{a}	0.2071
Ovate	0.0265^{c}	0.1972^{b}	0.3919^{a}	0.0001
Oblovate	0.0^{a}	0.0^{a}	0.0042^{a}	0.0716
PinatelyWedge	0.0^{a}	0.0^{a}	0.0016^{a}	0.0716
Achene	0.0170^{a}	0.0^{b}	0.0^{b}	< .0001
Berry	0.0011^{b}	0.8712^{a}	0.058^{b}	< .0001
CapsuleUtricule	0.0069^{b}	0.0752^{ab}	0.1636^{a}	0.0203
Caryopsis	0.3419^{a}	0.0^{b}	0.0^{b}	< .0001
Cone	0.0^{b}	0.0^{b}	0.2180^{a}	0.0062
Nut	0.0^{b}	0.0069^{b}	0.3178^{a}	< .0001
Nutlet	0.5710^{a}	0.0^{b}	0.0^{b}	< .0001
Samara	0.0^{b}	0.0464^{b}	0.2415^{a}	< .0001
Sori	0.0618^{a}	0.0^{b}	0.0^{b}	0.0002
Non-Dormant	0.0638^{a}	0.0707^{a}	0.1873^{a}	0.0038
MorphoPhysical	0.0^{a}	0.0^{a}	0.0027^{a}	0.7831
Physical	0.0^{a}	0.0^{a}	0.0^{a}	--
Physiological	0.9361^{a}	0.9258^{a}	0.8090^{a}	0.0404
MorphoPhyisio	0.0^{a}	0.0033^{a}	0.0008^{a}	0.4182
Non Vegetative	0.3289^{c}	0.9245^{a}	0.6065^{b}	< .0001
Vegetative	0.6710^{a}	0.0754^{c}	0.3934^{b}	< .0001
SpringFall	0.0552^{a}	0.0^{a}	0.0502^{a}	0.1239
SpringSummer	0.6002^{b}	0.3433^{c}	0.9078^{a}	< .0001
SummerFall	0.2718^{a}	0.0903^{b}	0.0190^{c}	< .0001
Fall	0.0725^{b}	0.5145^{a}	0.0^{b}	< .0001
Winter	0.0^{a}	0.0517^{a}	0.0228^{b}	0.2039

Table A.13. ANOVA results for assessment of traits across the bottom of functional types in Camp Williams, UT

Trait-Class	GSSgss 11	SHRshr 22	TREEtree 33	PR > F
MaxTotHt	2.093^{b}	2.0^{b}	8.928^{a}	< .0001
MaxVeght	0.3265^{b}	0.4529^{b}	1.2439^{a}	< .0001
Leaf Size	7.645^{b}	5.4701^{b}	13.23^{a}	< .0001
Seed Size	5.6769^{b}	2.6118^{c}	14.75^{a}	< .0001
Perennials	0.2895^{b}	1.0^{a}	1.0^{a}	< .0001
Annuals	0.7105^{a}	0.0^{b}	0.0^{b}	< .0001
Native	0.3347^{b}	1.0^{a}	1.0^{a}	< .0001
Introduced	0.6652^{a}	0.0^{b}	0.0^{b}	< .0001
Simple	0.9971^{a}	0.9777^{a}	1.0^{a}	0.1979
Compound	0.0028^{a}	0.0022^{a}	0.0^{a}	0.1979
Elliptic	0.0287^{b}	0.0^{b}	0.7732^{a}	< .0001
Needle	0.0^{b}	0.0^{b}	0.2267^{a}	0.0031
Fleshy	0.0^{a}	0.0073^{a}	0.0^{b}	0.0415
Lanceolated	0.0105^{a}	0.00513^{ab}	0.0^{b}	0.0967
Linear	0.7669^{a}	0.2225^{b}	0.0^{c}	< .0001
Oblong	0.1155^{a}	0.0022^{b}	0.0^{b}	< .0001
Ovate	0.0102^{a}	0.0^{b}	0.0^{b}	< .0001
Pinately	0.0679^{a}	0.0^{b}	0.0^{b}	< .0001
Wedge	0.0^{b}	0.7628^{a}	0.0^{b}	< .0001
Achene	0.0953^{c}	0.9904^{a}	0.7732^{b}	< .0001
Berry	0.0^{b}	0.0095^{a}	0.0^{b}	0.0079
Capsule	0.1101^{a}	0.0^{b}	0.0^{b}	< .0001
Caryopsis	0.6695^{a}	0.0^{b}	0.0^{b}	< .0001
Cone	0.0^{b}	0.0^{b}	0.2267^{a}	0.0031
Pod	0.1180^{a}	0.0^{b}	0.0^{b}	< .0001
Schizocarp	0.0069^{a}	0.0^{b}	0.0^{b}	0.0002
Non-Dormant	0.0432^{a}	0.0^{b}	0.0^{b}	< .0001
MorphoPhysical	0.0016^{a}	0.0^{b}	0.0^{b}	0.0299
Physical	0.0009^{a}	0.0^{a}	0.0^{a}	--
Physiological	0.8887^{b}	1.0^{a}	1.0^{a}	< .0001
MorphoPhyisio	0.0654^{a}	0.0^{b}	0.0^{b}	< .0001
Non Vegetative	0.8152^{b}	0.9904^{a}	0.2267^{c}	< .0001
Vegetative	0.1847^{b}	0.0095^{c}	0.7732^{a}	< .0001
SpringFall	0.0394^{a}	0.0^{b}	0.0^{b}	< .0001
SpringSummer	0.6135^{a}	0.0022^{b}	0.0^{b}	< .0001
SummerFall	0.3364^{b}	0.9977^{a}	1.0^{a}	< .0001
Spring	0.0105^{a}	0.0^{b}	0.0^{b}	0.0005
SpringWinter	0.0^{a}	0.0^{a}	0.0^{a}	--

Table A.14. ANOVA results to assess traits across the bottom of functional types in Camp Grayling, MI

Trait-Class	GSSgss 11	SHRUBgss 21	TREESgss 31	PR > F
MaxTotHt	1.325^a	1.854^a	1.55^a	0.2144
MaxVeght	0.307^b	0.39^b	0.555^a	0 .0020
Leaf Size	14.96^a	15.48^a	16.43^a	0.4292
Seed Size	2.0509^a	2.5095^a	1.9894^a	0.2605
Perennials	0.9772^b	1.0^a	0.993^{ab}	0.0849
Annuals	0.0227^a	0.0^b	0.0069^{ab}	0.0849
Native	0.9664^a	0.9465^a	0.9783^a	0.3128
Introduced	0.0336^a	0.0534^a	0.0216^a	0.3129
Simple	0.9374^a	0.8384^a	0.5977^a	< .0001
Compound	0.0626^b	0.1615^b	0.4022^a	< .0001
Elliptic	0.0781^b	0.1563^b	0.3897^a	< .0001
Needle	0.0^a	0.0^a	0.0^a	--
Lanceolated	0.0^a	0.0032^a	0.0019^a	0.6747
Linear	0.8942^a	0.8225^a	0.5709^b	< .0001
Oblong	0.001^b	0.00483^a	0.0^b	0.0065
Ovate	0.0265^a	0.0130^a	0.0373^a	0.8259
Oblovate	0.0^a	0.0^a	0.0^a	--
PinatelyWedge	0.0^a	0.0^a	0.0^a	--
Achene	0.0170^a	0.0074^a	0.0206^a	0.8287
Berry	0.0011^a	0.0102^a	0.0149^a	0.5514
CapsuleUtricule	0.0069^b	0.0206^a	0.0072^b	0.0592
Caryopsis	0.3419^a	0.3754^a	0.2365^a	0.1726
Cone	0.0^a	0.0^a	0.0^a	--
Nut	0.0^a	0.0^a	0.0^a	--
Nutlet	0.571^a	0.4398^{ab}	0.3332^b	0.0053
Samara	0.0^a	0.0^a	0.0^a	--
Sori	0.0618^b	0.1464^b	0.3807^a	< .0001
Non-Dormant	0.06^a	0.15^a	0.3695^b	0.7961
MorphoPhysical	0.0^a	0.0^a	0.00816^a	0.7182
Physical	0.0^b	0.0036^a	0.0^b	0.0434
Physiological	0.9361^a	0.8476^a	0.5976^b	< .0001
MorphoPhyisio	0.0^a	0.00072^a	0.0314^a	0.6310
Non Vegetative	0.3289^a	0.2291^a	0.2370^a	0.4643
Vegetative	0.6710^a	0.7708^a	0.7552^a	0.5828
SpringFall	0.0552^a	0.0493^a	0.0426^a	0.9504
SpringSummer	0.6002^a	0.4663^a	0.4193^a	0.0682
SummerFall	0.2718^b	0.3846^{ab}	0.5431^a	0.0014
Fall	0.0725^a	0.0997^a	0.0112^b	0.0027
Winter	0.0^a	0.0^a	0.0013^a	0.7975

CURRICULUM VITAE

Patricia Hernández-de la Rosa
(May 2002)

EDUCATION

1980-1984. Bachelor with a Major in Forestry. Universidad Autónoma Chapingo, Chapingo, México.

1988-1992 M.Sc. with emphasis in Silviculture and Management. Colegio de Postgraduados. Montecillo, México.

1996-2002. Ph.D. in Ecology (Forest Resources) (2002). Utah State University. College of Natural Resources. Forest Department. Logan, Utah, US.

WORK EXPERIENCE

1984 – 1988 Assistant Researcher. Colegio de Postgraduados. Forest Program. Montecillo, Mexico. Duties included developing, implementing, and evaluating research projects about regeneration, thinning, and logging in temperate forest.

1991 - 1998 Associate Researcher. Colegio de Postgraduados. Forest Program. Montecillo, Mexico. Duties included research in different projects related with conifer species in temperate forest, assistant in different forest courses at the graduate level.

1999 – currently. Titular Researcher. Forest Program. Montecillo, Mexico. Duties included research in different projects and teaching.

TEACHING EXPERIENCE (1992 – 2002)

Professor of Seminar I. Graduate level. Colegio de Postgraduados, Forest Program. Spring and Fall, 2002.

Professor of Silvicultural Systems. Graduate level. Colegio de Postgraduados, Forest Program. Spring, 1994 and 1995.

Assistant Professor of Analysis of Forest Ecosystems. Graduate level. Colegio de Postgraduados, Forest Program. Fall, 1994.

Assistant Professor of Silvicultural Theory. Graduate level. Colegio de Postgraduados, Forest Program. Fall, 1993.

Professor of Seminar II. Graduate level. Colegio de Postgraduados, Forest Program. Fall, 1992.

Assistant Professor of Regeneration Topics. Graduate level. Colegio de Postgraduados. Forest Program. Fall, 1992.

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