ABSTRACT

Title of Dissertation: DISTRIBUTION AND DYNAMICS OF THE EVERGREEN UNDERSTORY LAYER IN CENTRAL APPALACHIAN HIGHLAND FORESTS

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Evergreen understory layer communities dominated by *Rhododendron maximum* L. and/or *Kalmia latifolia* L. may exert significant controls on regeneration of overstory trees, carbon sequestration, and nutrient retention in central Appalachian forests, but their distribution and ecological importance are poorly understood at the regional scale. The distribution, temporal dynamics, and biomass of the evergreen understory layer were examined in the Ridge and Valley and Allegheny Plateau physiographic provinces in the mid-Atlantic Highlands using plot data, remote sensing, dendrochronology, and modeling. First, leaf-off satellite remote sensing and topographic data were applied to map the spatial extent and distribution of *R. maximum* and *K. latifolia* with better than 80 percent accuracy. Second, plot data were used to determine the relevant environmental factors and species associations related to the distributions of *K. latifolia* and *R. maximum* and assess their influence on forest vertical structure. Cluster analysis and ordination revealed that topo-edaphic gradients and intensity of gypsy moth defoliation were associated with differences in the distribution of these two shrub species within and between the two study areas, and midstory volume was significantly lower where evergreen understory coverage was continuous. Third, variation in *K. latifolia* and *R. maximum* growth rates were examined using remote sensing change detection and dendrochronology, and trends were compared to the timing of climatic fluctuations and gypsy moth defoliation of canopy trees. Remote sensing showed that patterns of evergreen understory growth vigor correlated with both defoliation and topographically mediated drought stress. Dendrochronology revealed considerable within-site variability among individual shrubs. However, both releases and suppressions in growth were associated with the timing of gypsy moth defoliation for *K. latifolia* in both provinces and for *R. maximum* in the Allegheny Plateau. Finally, carbon sequestration and nutrient storage impacts of these species were estimated by modeling their current aboveground biomass and ecosystem storage influences on several test watersheds. The inclusion of *K. latifolia* and *R. maximum* in the ecosystem model NuCSS indicated increases of up to 4825 kg/ha of carbon and 224 kg/ha of nitrogen storage, including notable increases of carbon and nitrogen in the forest floor and soil pools.

DISTRIBUTION AND DYNAMICS OF THE EVERGREEN UNDERSTORY LAYER IN CENTRAL APPALACHIAN HIGHLAND FORESTS

By

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Foreword

This dissertation document has been organized into six chapters. Chapter 1 serves as a general introduction, and includes overall research hypotheses, goals, rationales, and a review of previous research on *R. maximum* and *K. latifolia* and their ecological roles in Appalachian forests. The methods and results of four studies are reported in Chapters 2 through 5, which were written in the form of publishable manuscripts, with slight modifications made to enhance the flow of this document. Chapter 6 contains an overall review of research findings as well as a discussion of forest management implications related to evergreen understory communities.

Acknowledgements

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Table of Contents

List of Tables

List of Figures

Chapter 1: Research Objectives for the Examination of the Evergreen Understory Layer in Central Appalachian Forests

1.1 Introduction

Human societies rely on forest ecosystems to provide a number of services (Daily *et al*. 1997), among these are the maintenance of air and water quality, sediment trapping, flood attenuation, and nutrient storage (Perry 1998, Aber et al. 2000). Forests also act as carbon sinks capable of attenuating climatic changes caused by increases in atmospheric carbon (Schlesinger 1977, Sedjo 1992, Currie et al. 2003). In addition, forest ecosystems are valuable for providing habitat and refuge for wildlife, and are valued for their recreational and aesthetic characteristics. The future sustainability of these societal services depends on the welfare and successful management of forest ecosystems, which in turn entails a thorough understanding of the synecology of their component species.

In the eastern United States, the Appalachian highlands region contains one of the most extensive contiguous areas of forests, because the high amount of topographical relief has historically precluded their large-scale transformation into agricultural or urban land uses (Robison 1960). The broad scale relevance of the evergreen understory species rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) to Appalachian forests at landscape and coarser scales has not been studied extensively, despite their wide extent and prominent role in forest ecology where present. *R. maximum* and *K. latifolia* are important components of these forest ecosystems because they:

1) Have the potential for slowing mineral cycling (McGinty 1972, Thomas and Grigal 1976, Monk *et al.* 1985), and therefore have water quality maintenance implications in the event of disturbance. *R. maximum* has been referred to as a keystone species in this regard (Yeakley *et al*. 1994);
2) Inhibit canopy tree regeneration when present in dense stands (Minkler 1941, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al*. 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002);
3) Provide forage and refuge for wildlife (Romancier 1970, Gates and Harman 1980, Thackston *et al*. 1982, Johnson *et al*. 1995, Spear 1998, USDA 2002);
4) Are significant components of Appalachian forests with regard to carbon sequestration and nutrient budgets (McGinty 1972, Thomas and Grigal 1976, Monk *et al*. 1985);
5) Enhance the beauty and inspirational value of Appalachian forests (Hollenhorst *et al*. 1993);
6) Comprise part of the cultural and ethno-botanical heritage of the Appalachian region, with rhododendron and mountain laurel traditionally indicated for a number of medical uses (Sargent 1893, Uphof 1968), and used for craft items (e.g. one common name attributed to *K. latifolia* is ‘spoonwood’) (USDA 2002).

Because of the carbon sequestration and nutrient cycling implications of *K. latifolia* and *R. maximum* on the landscape scale, examination of their spatial extent and temporal dynamics is important, as they have been inadequately documented in past research. Their spatial extent and biomass amounts are also important in terms of their overall capacity to maintain water quality and mitigate climate change. In addition, the temporal dynamics of both leaf area (density) and spatial extent of the evergreen understory layer is relevant to its role in the inhibition of canopy tree regeneration, and hence the sustainability of the structure and function of Appalachian forest ecosystems for ecological, societal, and aesthetic values.

It has been estimated that roughly three million acres of forested land in the Southern Appalachian Mountains are covered by dense thickets of *K. latifolia* and *R. maximum* (Wahlenburg and Doolittle 1950), while *R. maximum* is said to be the dominant subcanopy species in an estimated 74 million acres in that region (Rivers *et al*. 1999). Moreover, the spatial extent and ecological importance of *R. maximum* and *K. latifolia* in the forests of the Appalachian region has steadily increased over the 20th century due to fire inhibition, logging, chestnut blight, and agricultural land abandonment (Dobbs 1995, Monk *et al*. 1985, Phillips and Murdy 1985, Baker 1994, Romancier 1970, Smith 1963). Specifically, the loss of chestnut provided not only light to the forest floor, but also removed an allelopathic agent (chestnut leaves), thereby supporting the release of *R. maximum* (Vandermast *et al*. 2002). There is some disagreement whether this expansion has occurred in *R. maximum* or *K. latifolia* understory communities (or both). For example, some have observed that the spatial extent of *R. maximum* has increased in the southern Appalachians, but that the cover of *K. latifolia* has remained stable (Dobbs 1995). Others have noted an increase in the acreage of dense stands of *K. latifolia* on xeric upper slope sites in the southern Appalachians resulting from high-grading of more desirable pitch pines and/or drought-related insect outbreaks (Elliott *et al*. 1999a, Waldrop *et al*. 2000). In the Central Appalachians, it has been observed that *R. maximum* is becoming more important, with thickets located in more mesic areas becoming denser and ones located in drier areas showing evidence of spreading (Plocher and Carvell 1987, McGraw 1989). Photointerpretation has been used to map *R. maximum* and *K. latifolia* in the southern Appalachian Mountains and provide evidence of its spatial dynamics over time (Dobbs 1995), but no automated procedure has been developed to document this phenomenon using increasingly available, inexpensive, and repeatable multispectral remote sensing data. The mapping, estimation of biomass, and tracking of temporal dynamics in evergreen understory plant communities on the landscape and regional scales is a valuable application of multispectral remote sensing and GIS modeling, and would be of great value for forest managers.

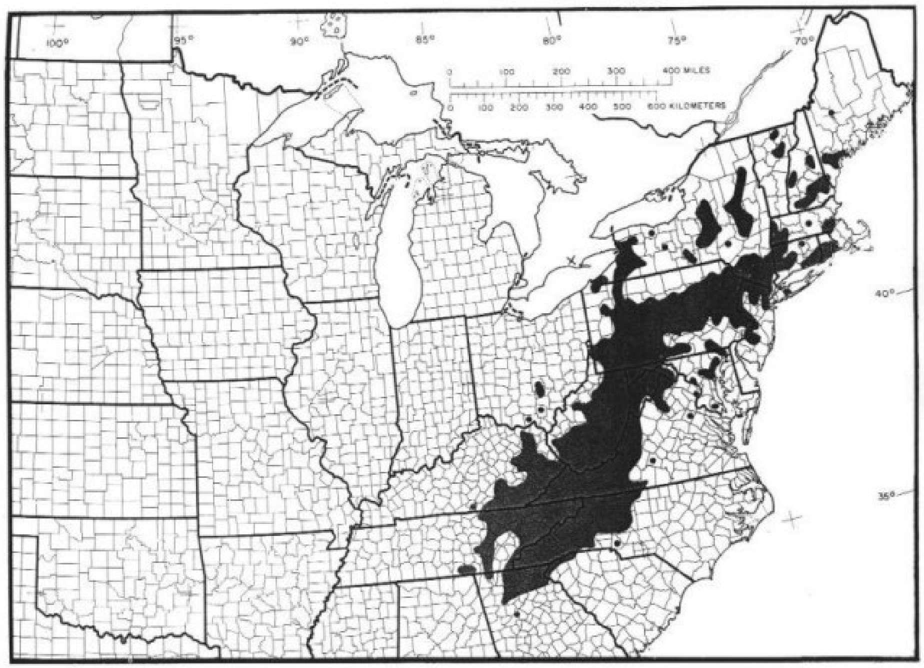
1.2 Previous Research

The presence of *K. latifolia* and *R. maximum* thickets in the understory layer of the forests of the southern and central Appalachian Mountains brings about long-term changes in forest structure and composition. These changes result primarily from declining survivorship of regenerating canopy trees during the risky seedling phase due to intense competition for resources with evergreen understory shrubs, which is often conspicuously inflated when plant density is high (Harper 1967, Nilsen *et al.* 2001). Secondary effects of the presence of a dense evergreen understory layer include reduced seed rain, inhibited mycorrhizal synthesis, and lower bacterial or invertebrate activity related to the deep and slowly decaying litter typical under thickets (Rivers *et al*. 1999, Walker *et al*. 1999). The impact of evergreen understory shrub thickets on canopy tree seedling regeneration failure has been examined at the plot level in a number of studies (Nilsen *et al.* 2001, Beckage *et al.* 2000, Nilsen *et al.* 1999, Walker *et al*. 1999, Baker and Van Lear 1998, Clinton and Vose 1996, Waterman *et al.* 1995, Clinton *et al.* 1994, Monk *et al.* 1985, Phillips and Murdy 1985). In addition, the composition of woody and herbaceous plant species in the regeneration layer is less diverse with the presence of *R. maximum* (Hedman and Van Lear 1995, Baker 1994, Baker and Van Lear 1998 Vandermast and Van Lear 2002) and *K. latifolia* (Waterman *et al*. 1995, Ducey and Moser 1996, Elliott *et al* 1999a, 1999b, Clinton and Vose 2000, Waldrop *et al*. 2000). Finally, it has been observed that the structure of forests where the understory layer is dominated by *R. maximum* and/or *K. latifolia* is less complex than in forests that do not contain thickets of these species (Hedman and Van Lear 1995). For example, Baker and Van Lear (1998) report that the riparian forest sites in their study were essentially two tiered forests with an overstory dominated by *Betula* species and an understory effectively dominated by *R. maximum*. With the wealth of plot-scale studies of the effects of *R. maximum* and *K. latifolia* on forest regeneration, it is surprising that there has not been more research on the comprehensive landscape- and regional-scale effects of the evergreen understory layer on forest structure and functioning (*sensu* Whittaker 1962, Thomas and Grigal 1976, Monk *et al*. 1985).

There are notable dissimilarities in the geographical ranges, ecological niches, and consequent management implications for *R. maximum* and *K. latifolia*. For example, the geographic range for *K. latifolia* is much broader compared to that of *R. maximum* (Figures 1.1 and 1.2). Also, the ecological niches for *R. maximum* and *K. latifolia* are dissimilar, with *R. maximum* encountered in sheltered areas with abundant moisture and *K. latifolia* found more commonly on exposed upper slopes and ridges. The different landscape positions inhabited by these two species are caused by differences in their responses to solar radiation, cold air drainage, soil moisture, summer and winter temperature regimes, and atmospheric drying potentials (Dobbs 1995, Monk *et al.* 1995, Muller 1991, Lipscomb and Nilsen 1990a, 1990b). Because of their unique qualities, *R. maximum* and *K. latifolia* are discussed separately below.

1.2.1 Rhododendron maximum

Rhododendron maximum grows primarily in the mountainous regions of eastern United States from western Maine to Georgia (Figure 1.1), with disjunct populations also found in New England, Kentucky, Tennessee, and Ohio (USDA 2002). At the edges of its range, *R. maximum* can be found growing in increasingly atypical landscape positions. For example, *R. maximum* has been observed growing in New England in poorly drained environments, often associated with Atlantic white cedar (*Chamaecyparis thyoides*) (Spencer 1932, Vogelmann and Charette 1963). Also, *R.*



Map 119. *Rhododendron maximum* L., rosebay rhododendron.

Figure 1.1: The geographic Range of *Rhododendron maximum* in North America (from Little 1977).

maximum has been reported growing only along rock walls in Ohio (Mills 1972).

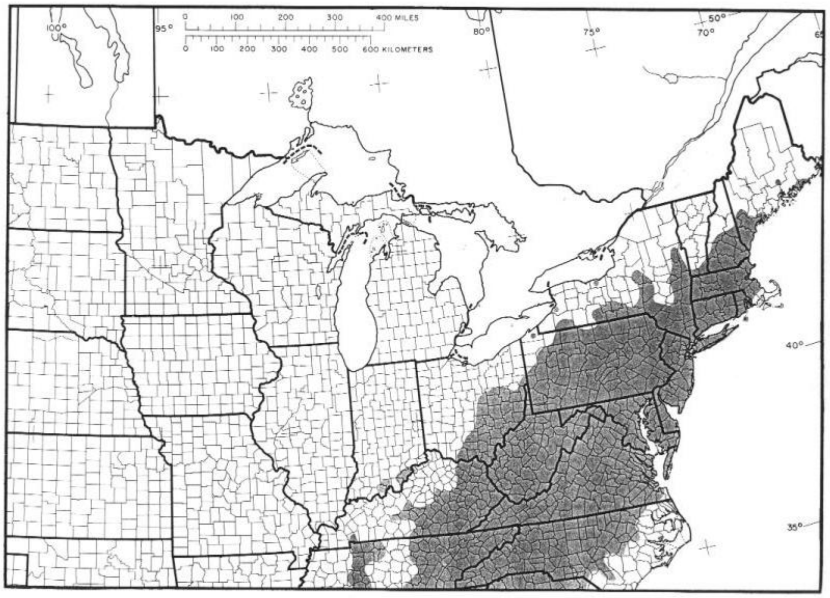
Although *R. maximum* is clearly sensitive to high irradiance (Nilsen *et al*. 1988, Lipscomb and Nilsen 1990a), it has a relatively wide ecological amplitude (Baker 1994, Rivers *et al*. 1999), and "no one physiographic situation confines *R. maximum* as long as moisture is abundant" (Hogdon and Pike 1961). Land use and disturbance factors such as fire, agricultural, logging, and the chestnut blight influenced patterns currently seen in *R. maximum* density and abundance (Woods and Shanks 1959, Baker 1994, Vandermast *et al*. 2002). Although *R. maximum* is associated with riparian zones, moist coves, and north-facing slopes, this drought susceptible shallow-rooted plant can be found in other areas with sufficient moisture availability (Romancier 1970, Monk *et al.* 1985, Plocher and Carvell 1987, Lipscomb and Nilsen 1990a, 1990b, Muller 1991). In the Southern Appalachians, *R. maximum* has been observed to form dense stands in mesic cove forest environments, but is consistently present in scattered clumps in mid-slope areas as well (Keever 1953). Whittaker (1962) describes *R. maximum* as growing from low to middle elevations and from mesophytic forests to heath balds in the Southern Appalachians. The development of heath balds is not replicated in the Central Appalachians because rainfall amounts are not sufficient for *R. maximum* to grow in large thickets anywhere but in more protected, mesophytic environments. *R. maximum* does occur on ridge top sites in the Allegheny Plateau of the Central Appalachian Mountains, but primarily where protection against desiccation and quick freeze/thaw transitions is afforded by large rock walls (Mills 1972) or where seeps provide ample moisture to maintain deep wet organic soils (Townsend, pers. comm.). *R. maximum* does not commonly form large thickets at these locations, however.

Interactions between the growth habits of *R. maximum*, land use and disturbance history, and herbivory are rather complex, and may act to limit the spatial extent of this species' realized niche in Appalachian forests. *R. maximum* requires a high light environment and moss seedbeds for successful seedling establishment (Smith 1963, Romancier 1970, USDA 2002). In contrast, mature *R. maximum* is sensitive to elevated irradiance (Lipscomb and Nilsen 1990b). The conditions under which *R. maximum* will become established can therefore be initiated by disturbances such as logging (McGee and Smith 1967, Romancier 1970), canopy tree death (Phillips and Murdy 1985), or the abandonment of agricultural land (Romancier 1970). The flood of sunlight and presence of nurse logs after logging or a canopy gap opening allows *R. maximum* seedlings to become established, and regrowing trees then provide shade for maturing *R. maximum* individuals. *R. maximum* individuals can produce more than 100,000 to 500,000 seeds in a single year (Romancier 1970, Cooper and McGraw 1988), and its seedlings may grow within a considerable range of pH, but are inhibited by the presence of calcium (Romancier 1970). Because seeds of *R. maximum* are small and scale-like and not likely to be dispersed far by the wind (Knowlton 1950), seed availability poses another limitation to its ability to spread to new areas. Seedling recruitment is an important reproductive pathway during the early colonization of *R. maximum*, but ramet layering dominates in the interior of dense populations while seedling establishment continues only on the edges of established thickets (Romancier 1970, Plocher and Carvell 1987, McGraw 1989, Pornon and Doche 1995, USDA 2002). Finally, it is believed that changes in fire regimes have caused this evergreen understory species to become more widespread and dense in existing patches, but that deer herbivory has kept expansion to new patches somewhat in check (Romancier 1970, Johnson *et al*. 1995).

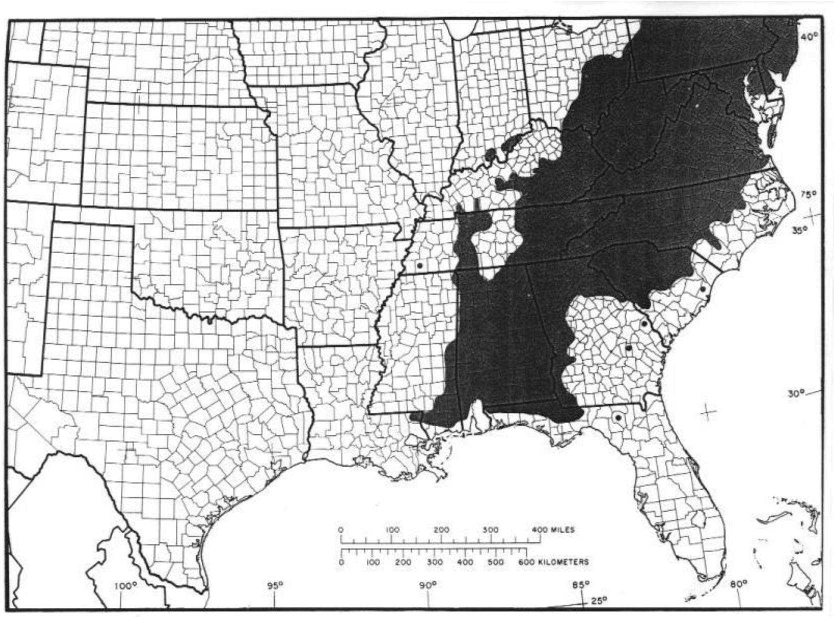
The ecological importance of *R. maximum* in forested ecosystems is based in part in its ability to lock up the available nutrients in a forest stand. Indeed, part of the success of this species can attributed to the conservative growth strategy related to its evergreen habit. The long-lived and slowly decomposing *R. maximum* leaves further retard tree seedling regeneration by limiting nutrient availability in the system (Baker 1994, Beckage *et al*. 2000). For example, between 13 and 34 percent of the total ecosystem leaf nutrient standing crop was estimated to be retained annually in *K. latifolia* and *R. maximum* leaves and litter in one southern Appalachian watershed (Monk *et al*. 1985). This inordinate accumulation of nutrients is made possible because *R. maximum* leaves survive from 3 to 7 years depending on characteristics of the microclimate (Bao and Nilsen 1988), with shorter leaf persistence observed in *R. maximum* individuals growing in exposed, high irradiance environments compared to more shaded locations (Whittaker 1962, Nilsen 1986, Nilsen *et al*. 1987). In addition, *R. maximum* leaf litter decays three times slower than typical deciduous canopy tree leaves (Thomas and Grigal 1976, Webster, pers. comm.).

1.2.2 Kalmia latifolia

Mountain laurel (*K. latifolia*) is widely distributed in eastern North America, and can be found from New Brunswick to northern Florida (Figure 1.2). It occurs primarily along the Appalachian Mountains, westward to Louisiana and northward into southern Ohio and Indiana (USDA 2002). *K. latifolia* presents problems for timber management on millions of acres in the southern Appalachians when dense thickets that develop after timber harvest or due to changes in the fire regime reduce the growth of tree seedlings and threaten the regeneration of canopy tree species (Waterman *et al*. 1995, USDA 2002). Lightning and human caused fires have historically maintained ridge top pine communities, which are becoming increasingly rare in the southern Appalachians (Waldrop *et al*. 2000). These communities typically consist of an overstory of table mountain pine or pitch pine, a midstory of chestnut oak, scarlet oak, and blackgum, and a dense shrub layer of *K. latifolia*. If left alone, the oak and blackgum midstory species eventually replace the current pine canopy species. Management strategies employed to maintain these ridge top pine communities have typically prescribed felling the canopy and burning the excess evergreen understory growth (Hooper 1969, Ducey *et al*. 1996, Meyer and Swank 1996, Elliott *et al*. 1999a, 1999b, Clinton and Vose 2000). This treatment initially reduces the abundance of *K. latifolia* and delays its growth, so that pine seedlings can



Map 75-NE. *Kalmia latifolia* L., mountain-laurel.



Map 75-SE. *Kalmia latifolia* L., mountain-laurel.

Figure 1.2: The geographic Range of *Kalmia latifolia* in North America (from Little 1977).

sprout before the *K. latifolia* resprouts and out-competes these seedlings. *K. latifolia* eventually returns to dominate the understory, but not before a cohort of canopy replacing pine seedlings becomes established above the height of the regrowing *K. latifolia* (Hooper 1969, Elliott *et al* 1999a). As an added advantage associated with burning, the nutritional quality of *K. latifolia* leaves has been observed to increase in recently burned areas, providing improved forage for deer and ruffed grouse (Thackston *et al*. 1982, USDA 2002).

K. latifolia exhibits reduced photosynthetic performance and water use efficiency under low irradiance conditions (Lipscomb and Nilsen 1990b). *K. latifolia* stem growth under higher light conditions has been found to be three times that observed under low light conditions (Davidson 1966). *K. latifolia* therefore typically grows on more exposed sites compared to *R. maximum*, such as upper slopes and ridge tops (Monk *et al*.1985, Lipscomb and Nilsen 1990a, 1990b, Muller 1991). Whittaker (1962) describes *K. latifolia* as growing at lower and middle elevations in chestnut oak heaths and in lower elevation mixed heath balds in the southern Appalachian Mountains. It also occurs widely in less mesophytic forest types. *K. latifolia* grows in the midst of *R. maximum* thickets under canopy gaps due to its rapid sprouting ability. The smaller leaves of *K. latifolia* compared to *R. maximum* allow *K. latifolia* to survive the leaf-off winter periods on exposed sites without damage from high irradiance (Lipscomb and Nilsen 1990a). Moreover, the stomata open and *K. latifolia* is photosynthetically active during warm winter days (Nilsen 1992).

K. latifolia regenerates both sexually and asexually. The pollination mechanism of *K. latifolia* is unique, with tension in the filaments of the flower releasing when the tongue of a bee is inserted in the crevis between the ovary and stamens. This causes pollen to be thrown onto the head of the bee, where it is carried to the stigma of the next flower visited (USDA 2002). The small seeds are disseminated a short distance by wind, but their preference for short moss seedbeds or moist mineral soil restricts seedling production to relatively small areas. Wilson and O'Keefe (1983) suggest an association between the landscape-scale pattern of *K. latifolia* and past land use in second growth forests, as moss seedbeds are slow to recover following agricultural activity, which hinders the re-invasion of *K. latifolia* after abandonment. As a consequence, *K. latifolia* is found abundantly in rocky areas and swamps that have never been cleared for agriculture and therefore acted as refugia for *K. latifolia* (Wilson and O'Keefe 1983). Due to these limitations, *K. latifolia* regenerates primarily by sprouting from the root collar, by rhizomes, and by layering (Wilson 1997, USDA 2002).

1.3 Study Areas

Two study areas were delimited to assess the spatial extent and potential ecological influence of the evergreen understory species *R. maximum* and *K. latifolia* in central Appalachian highland forests (Figure 1.3). These areas were selected for their differing topographic and climatic environments. One study area is located in the warmer and drier Ridge and Valley physiographic province (encompassing the Green Ridge and Buchanan State Forests in Maryland and Pennsylvania), and the other is

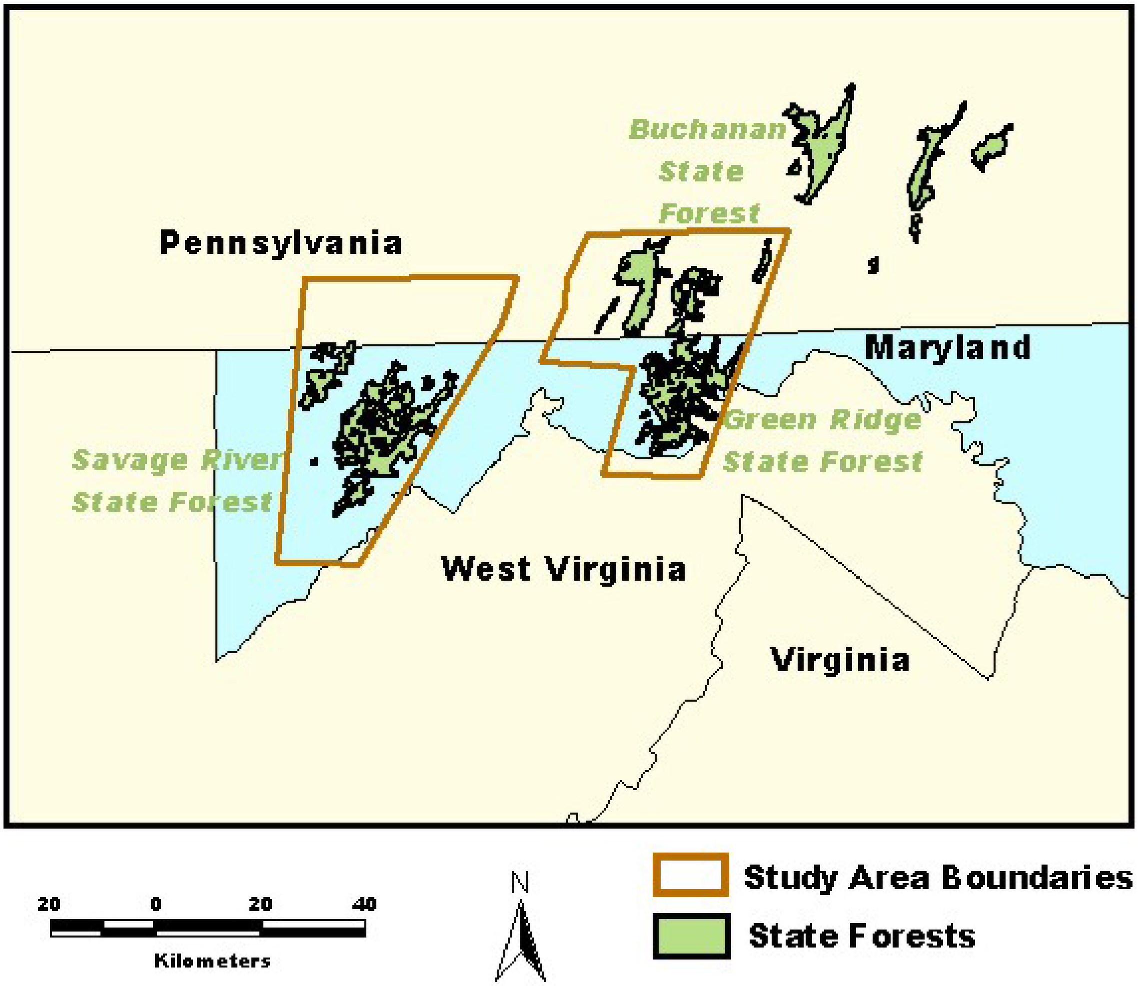


Figure 1.3: Area map of present study showing extent of state forest lands.

located on the cooler and wetter Allegheny Plateau (containing the Savage River, Potomac, and Forbes State Forests). A considerable extent of these study areas is designated as public forest or game lands, and consequently experience less intensive development and logging pressure than adjacent privately held land. Because of differences in topography and climate, disturbance, and land use history, the forest community composition and structure of the forest communities in these two study areas are dissimilar from each other, but are representative of a broad range of environmental conditions typically found in the central Appalachian region. Both study areas are located in the heart of the geographic range of *K. latifolia* and *R. maximum* (Figures 1.1 and 1.2), and are described in more detail below.

1.3.1 Ridge and Valley Study Area

This study area lies in the Ridge and Valley physiographic province in western Maryland and south-central Pennsylvania, and consists of two large state forest areas – Green Ridge State Forest (GRSF) and Buchanan State Forest (BSF). The majority of the evergreen understory vegetation found in this study area is located in BSF, with the largest concentration located in an area known as the Martin Hill Wild Area (4450 ha). The forests within the Martin Hill Wild Area were originally harvested in the late 1800s and early 1900s, and although some timber harvesting has occurred in recent years, it represents only a small portion of the entire area. The area of BSF that lies within the Pennsylvania portion of the study area boundary is 12,142 ha, and was acquired by the state between 1904 and 1930. Additional Pennsylvania public lands within this study area include the Western Pennsylvania Conservancy Sideling Creek preserve (70 ha) and state game lands (6594 ha).

The GRSF area in Maryland was heavily cut for timber, tanbark, and hoop poles between 1879 and 1910, and wildfires were common in the regenerating forest for a number of years thereafter (Mash 1996). During the period of heavy forest product exploitation, numerous towns grew up in this region as well as two railroad lines to transport timber, goods, and passengers. In the early and middle 20th century, much of the area that is now the GRSF was planted in fruit (primarily apple) orchards (Mash 1996). The intense land use history within the GRSF has influenced current forest composition, which is largely devoid of *K. latifolia* and *R. maximum*. Between 1937 and 1948, and again in the early 1970s, the state of Maryland purchased most of the land developed as orchards, bringing the total land area of the GRSF to 17,363 ha.

The current forest of the ridge and valley study area is composed primarily of deciduous trees, mixed with a lesser amount of coniferous trees in the canopy. Field data from this research indicate that chestnut oak (*Quercus prinus*) comprises 24 percent of the total basal area, followed by red oak (*Quercus rubra*) at 16 percent, white oak (*Quercus alba*) at 13.5 percent, scarlet oak (*Quercus coccinea*) at 7.5 percent, and black oak (*Quercus velutina*) at 6.5 percent (unpublished data). Various pines (*Pinus virginiana, strobus, rigida, and pungens*) make up 9 percent of the overall basal area in this study area. These forests are largely 50 to 75 years in age (Maryland Continuous Forest Inventory, unpublished data).

Yearly average minimum and maximum temperatures for this study area are 2.3 and 15.8°C, with temperatures rarely exceeding 32°C in the summer months, but regularly dipping below -10°C in the winter (Stone and Matthews 1974). Elevation ranges from 123 to 845 meters, with steep northeast-southwest trending ridges in the GRSF and a larger contiguous upland area in the Martin Hill section of the BSF. The annual precipitation range was 896 – 1297 mm (averaging 1023 mm) for the period 1983-1998. The soils in the GRSF area include the Weikert-Gilpin and Weikert-Calvin-Lehew associations. In the BSF, the Hazleton-Dekalb-Buchanan association predominates. All of these series are rather acidic, with a pH between 4 and 5.5. The Weikert soil series are rather shallow, and form on rolling and very steep ridges from weathered acid shale and siltstone and some fine-grained sandstone. The Wiekert series is the most extensive, covering approximately 30 percent of the area (Stone and Matthews 1977). The Gilpin soil series are moderately deep, and form from weathered acid shale and siltstone and some fine-grained sandstone. The Calvin and Lehew series are moderately deep, and form from weathered red or reddish shale, siltstone, or fine-grained sandstone (Stone and Matthews 1977). The Hazleton, Dekalb, and soil series are deep to moderately deep and form from sandstone residuum on convex upland plateaus, ridge tops and shoulder slopes, whereas Buchanan soils occur on foot slopes and have a fragipan layer (Stone and Matthews 1977).

1.3.2 Allegheny Plateau Study Area

The Allegheny Plateau study area is considered part of the mixed mesophytic forest by Braun (1950). As with the ridge and valley, this area was largely cut in the 20th century, but has regenerated naturally in the interim. The bulk of the public land located within this study area is the 24,401 hectares of land designated as the Savage River State Forest (SRSF), with a smaller holding designated as Potomac State Forest (1187 ha) and a section of Forbes State Forest in Pennsylvania (2479 ha). A total of 3579 hectares of state game lands also exist in the Pennsylvania portion of this study area. The forest canopy in this study area is primarily deciduous with localized areas dominated by eastern hemlock (*Tsuga canadensis*). Data from a systematic sampling of species composition that was performed in 105 field plots indicate that red oak (*Quercus rubra*) makes up 25 percent of the total basal area, followed by red maple (*Acer rubrum*) at 18 percent and chestnut oak (*Quercus prinus*) at 17 percent (unpublished data). Hemlock accounts for 5.5 percent of the total basal area. American chestnut was an important component of these forests previous to its extirpation in the early to mid 20th century due to the blight caused by the fungus *Cryphonectria parasitica* (Braun 1950).

The Allegany Plateau study area is characterized by a humid continental climate with severe winters and mild summers. The annual precipitation range between 1983 and 1998 was 913 – 1490 mm, with an average of 1216 mm. The soils characteristic of this area are strongly weathered and acidic, with a pH between 4 and 6. They are formed primarily by accumulated residuum due to the *in situ* weathering of parent material (Stone and Matthews 1974), with the Dekalb-Calvin-Gilpin soil association predominating. The elevation range for this study area is 304 to 986 meters.

1.4 Research Objectives and Overall Hypotheses

The central goal of this research is to examine the prevalence, ecological impacts and potential future influence of a dense evergreen understory coverage within two concentrated areas located in separate physiographic provinces representative of conditions in the central Appalachian highlands. This entails the examination of 1) relationships between forest community composition and structure and the presence of a significant evergreen understory layer, 2) the spatial distribution of the evergreen understory layer, 3) factors associated with its temporal dynamics over a 16 year period for which remote sensing imagery data are available, and 4) the importance of *R. maximum*- and *K. latifolia*-dominated understories with respect to carbon sequestration and nutrient dynamics on a landscape scale. These individual research aims are pursued in order to gain a comprehensive understanding the total impact of *R. maximum*- and *K. latifolia*-dominated understory communities on forest ecosystem services on the landscape scale, and is intended to inform decisions made by forest managers regarding the significance of forest stands containing these understories so that well-informed adaptive management strategies can be assembled.

General hypotheses to be tested include:

1) Forest composition and structure in the forests of the central Appalachian highlands are related to the amount of coverage of the evergreen understory

layer, and these characteristics are different from forests that do not contain an evergreen understory. This is caused by the inhibition of canopy tree regeneration by dense evergreen understories;

2) Evergreen understory communities are persistent, but variable over time. Specifically, disturbance due to gypsy moth defoliation and subsequent canopy tree death positively influences (releases) the growth and hence the leaf area of *K. latifolia*, while suppressing growth of *R. maximum* due to changes in the light environment in the understory. In addition, growth is suppressed in both species due to periodic drought pressure;
3) *R. maximum*- and *K. latifolia*-dominated understory communities are significant components of the forests of the central Appalachian highlands with respect to carbon sequestration and nutrient cycling dynamics.

1.5 Methods

The relationships between forest community composition and structure and the coverage of *R. maximum* and/or *K. latifolia* are examined using field survey data collected at 105 vegetation plots established in the Allegheny Plateau and 108 plots were placed in the Ridge and Valley province. These data include structural (tree and strata heights, leaf area, etc), compositional (basal area, cover by species, etc), and environmental measurements (indirect gradients inferred from geomorphology, geology, soil type, etc). Clustering analysis and non-metric multidimensional scaling (NMS) are used with the survey data to differentiate controlling environmental factors of forest communities between the two study areas. ANOVA is employed to examine differences between the mid-story volume of canopy tree species in areas with an evergreen understory versus areas where it is absent. Inhibition of canopy tree regeneration caused by an extensive coverage of evergreen understory species is assumed to be manifest as a comparatively smaller volume of trees in the midstory.

The current spatial extent of the evergreen understory layer is determined using remotely sensed data combined with topographic information. Additional ancillary information sources are also applied to improve the classification accuracy of the evergreen understory community map, and different classification strategies are tested to assess the relative strengths of different approaches. Specifically, the utility of synthetic aperture radar (SAR) and hyperspectral image data is examined using various supervised classification decision rules (maximum likelihood and minimum distance) and classification trees. The creation of a highly accurate evergreen understory community map is critical, as it serves as a foundation for further research goals.

Changes in the spatial characteristics of evergreen understory communities over time is investigated using change vector analysis (Lambin and Strahler 1994, Johnson and Kasischke 1998, Allen and Kupfer 2000, 2001). Specifically, changes in the vectors of brightness, greenness and wetness indices derived from a time series of remotely sensed images are examined, then validated using growth increment data obtained from stem samples of *R. maximum* and *K. latifolia*. Dates of apparent growth suppressions and releases are compared to the timing of gypsy moth infestation and climatic fluctuations. The temporal dynamics of the leaf area (density) of *R. maximum* and *K. latifolia* may suggest an alternative hypothesis to the apparent regeneration bottleneck caused by persistent evergreen understory communities, in that periods of attenuated growth vigor and decreased leaf area may give rise to phases of enhanced canopy tree regeneration.

The impact of the evergreen understory layer on nutrient cycling and carbon sequestration is investigated through the use of the Nutrient Cycling spreadsheet (NuCSS) model (Verburg and Johnson 2000). The NuCSS model is parameterized using soil, atmospheric deposition, vegetation, and forest floor compartments to simulate C, N, and P cycling in both the Plateau and Ridge and Valley study areas. Average shrub stem diameters are calculated for both *R. maximum* and *K. latifolia* so that the biomass of these species can be estimated using allometric equations (*sensu* McGinty 1972, Monk *et al*. 1985). Stem density data is then regressed against an index derived from remote sensing data (tasseled cap greenness) to extrapolate the density of the evergreen understory layer in locations classified as *R. maximum*, *K. latifolia*, and 'mixed' evergreen understory across both study areas. Plant growth as well as decomposition and N mineralization are calculated annually for a 50-year simulation. The forests in both study areas are parameterized in initial NUCSS model runs as simple deciduous forest stands (with a conifer component) based on the species importance values obtained from field survey data. Then the evergreen understory layer is added (with amounts based on areal extents determined from the remote sensing classification) to this simplified forest for further model runs, and differences in carbon sequestration and nutrient dynamics between these two idealized forest types are examined.

1.6 Summary

Each of the research aims described above are examined in the following chapters, with chapter 6 providing a synoptic overview and conclusions. In chapter 2, forest compositional and structural implications related to the presence of an evergreen understory layer are examined. Chapter 3 focuses on the use of remote sensing techniques to determine the spatial distribution of the evergreen understory layer in the two study areas examined. In Chapter 4, relationships between the growth vigor and leaf area of evergreen understory communities and the timing of gypsy moth defoliation events and climatic fluctuations are investigated. Chapter 5 addresses the carbon sequestration and nutrient cycling implications of *R. maximum* and *K. latifolia* in the central Appalachian highlands.

These separate research trajectories are being pursued to further our understanding of the principal landscape scale impacts of evergreen understory layer communities dominated by *R. maximum* and/or *K. latifolia* in the central Appalachian highlands region. First, landscape-scale validation of the relationships observed on a plot scale between the composition and structure of forests and the presence of a dense evergreen understory layer sets the stage for a regional analysis. Second, assessment of the potential for multispectral remote sensing data to discern forest evergreen understory communities will be a valuable contribution to forest monitoring science in general, and testing the utility of ancillary data to increase the accuracy of evergreen understory community identification on landscape to regional scales will further enlighten future forest remote sensing studies in the central Appalachian highlands region. Third, examination of potential associations between gypsy moth defoliation and climatic fluctuations and the dynamics of *R. maximum* and *K. latifolia* growth may suggest a pathway to canopy tree regeneration where a dense evergreen understory layer exists, providing an explanation for why central Appalachian forests with these understories do not regress wholesale into shrublands. Finally, the investigation into the carbon sequestration and nutrient cycling implications of *R. maximum*- and *K. latifolia*-dominated understory communities across the two study areas will illustrate the importance of this often-overlooked component of Appalachian forests to ecosystem functioning. Taken together, the results of this research are intended to provide information relevant to forest management in the central Appalachian highlands region regarding the impacts (good and bad) of the evergreen understory layer on the functioning of these forests.

Chapter 2: Role of the Evergreen Understory Layer in the Forest Vegetation Communities of the Central Appalachian Highlands

Abstract

Evergreen understory communities dominated by *Rhododendron maximum* L. and/or *Kalmia latifolia* L. may exert significant controls on regeneration of overstory trees, carbon sequestration, and nutrient retention in central Appalachian forests, but the regional distribution and ecological influence of these communities are poorly understood. I employed leaf-off satellite remote sensing combined with field sampling and quantitative analyses to assess patterns of *R. maximum* and *K. latifolia* distribution. Comparisons of species distributions in the warmer and drier Ridge and Valley physiographic province and on the cooler and wetter Allegheny Plateau indicate that spatial patterns were mediated by land use history and topography, respectively. Cluster analysis and non-metric multidimensional scaling (NMS) of plot survey data revealed that *R. maximum* and *K. latifolia* varied from each other in their species associations, and that topographic exposure, relative wetness, and intensity of gypsy moth defoliation were the chief environmental variables associated with differences in distribution within and between the two study areas. ANOVA demonstrated significant differences in midstory volume, basal area, and leaf area of canopy tree species where evergreen understory species were prominent, indicating that these communities substantially influence overall forest structure, stand dynamics, and regeneration. Specifically, basal area and leaf area were lower above *K. latifolia* understory communities, and midstory volume was found to be lower in areas where *K. latifolia* and *R. maximum* were abundant. However, the results show that cover of *K. latifolia* must be sufficiently continuous (i.e. not patchy) for the midstory volume to be affected. In plots with a history of gypsy moth infestation, basal area was found to be significantly lower in plots where *K. latifolia* thickets were present than where it was absent, suggesting that *K. latifolia* retards structural recovery from this disturbance. Finally, the amount of *Acer rubrum* present in the midstory layer far exceeded that found in the canopy layer, indicating that *A. rubrum* may be increasing in prominence. This inequality was less marked in areas where *K. latifolia* and/or *R. maximum* were present.

2.1 Introduction

The Appalachian highlands region (39° 54’N, 79°18’W by 39°26’N, 78°15’W) contains extensive contiguous areas of forests. This is due in part to the high topographic relief, which has precluded broad-scale transformations to agricultural or urban land uses (Robison 1960). The forest ecosystems in the Appalachian highlands provide a number of significant societal services (Daily *et al*. 1997), including the maintenance of air and water quality, sediment retention, flood attenuation, and nutrient storage (Perry 1998, Aber *et al*. 2000). On the global scale, forested areas such as these also act as a carbon sink capable of attenuating climatic changes by sequestering atmospheric carbon (Schlesinger 1977, Sedjo 1992, Currie *et al*. 2003). Appalachian forests also provide important habitat for wildlife, and are valued for their recreational and aesthetic characteristics. The future sustainability of these societal services depends on the welfare and successful management of forest ecosystems, which in turn entails a thorough understanding of the distribution of individual species and associations of species in these forest communities.

The broad-scale relevance of two evergreen understory species, rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) to Appalachian forests at landscape and broader scales has not been adequately addressed in the literature, despite their wide geographic extent and prominent role in forest ecology. *R. maximum* and *K. latifolia* occur in forest understories in nearly pure stands or mixed in varying proportions and have been mapped on the landscape scale in the southern Appalachian Mountains (Dobbs 1995), but in the central Appalachians only plot level analyses of their reproductive behavior and ecological relationships have been performed (Plocher and Carvell 1987, Cooper and McGraw 1988). Their locations are correlated with topography, with *R. maximum* typically found in protected, mesic locations and *K. latifolia* more often located on exposed, upslope sites. The different landscape positions inhabited by these two species are characterized by differences in solar radiation, cold air drainage, soil moisture, summer and winter temperature regimes, and atmospheric drying potentials (Davidson 1966, Monk *et al.* 1985, Plocher and Carvell 1987, Lipscomb and Nilsen 1990a, 1990b, Muller 1991, Dobbs 1995). Previous work suggests that *R. maximum* and *K. latifolia* are important component species of Appalachian forests because they:

1) Have the potential for slowing the cycling of N and P by accumulating these minerals in their evergreen leaves that become recalcitrant litter (McGinty 1972, Thomas and Grigal 1976, Monk *et al.* 1985), and therefore have water quality maintenance implications in the event of disturbance. *R. maximum* has been referred to as a keystone species in this regard (Yeakley *et al*. 1994);

2) Inhibit canopy tree regeneration when present in dense stands (Minkler 1941, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al*. 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002);

3) Provide forage and refuge for wildlife (Romancier 1970, Gates and Harman 1980, Thackston *et al*. 1982, Johnson *et al*. 1995, Spear 1998, USDA 2002);

4) Are significant components of Appalachian forests with regard to carbon sequestration and nutrient budgets (McGinty 1972, Thomas and Grigal 1976, Monk *et al*. 1985);

5) Enhance the beauty and hence inspirational value of Appalachian forests (Hollenhorst *et al*. 1993); and

6) Comprise part of the cultural and ethno-botanical heritage of the Appalachian region, traditionally indicated for a number of medical uses (Sargent 1893, Uphof 1968) and used for craft items (e.g. one common name attributed to *K. latifolia* is 'spoonwood') (USDA 2002).

The objectives of this study are to examine how the floristic and structural characteristics of forests in two physiographic provinces located in the central Appalachian highlands are associated with the presence of evergreen understory communities dominated by *R. maximum* and/or *K. latifolia*. Cluster analysis is used to classify forest community types from vegetation field survey data, ordination is employed to identify the emergent gradients that influence community distributions, and analysis of variance (ANOVA) is used to examine how the presence or absence of an evergreen understory layer related to forest vertical structure. Secondarily, the relationship between forest canopy defoliation history and forest structure is investigated. Finally, red maple abundance in the canopy and subcanopy is examined to determine whether disparities in composition exist that might suggest ongoing compositional change. Hypotheses tested during these analyses include:

1) Forest structure is simplified by the presence of the evergreen understory layer. Specifically, the inhibition of canopy tree regeneration by a continuous evergreen understory layer (e.g. when the cover is not patchy) is manifest by a relatively smaller midstory volume; and

2) Different environmental factors influence the pattern of forest communities in general and evergreen understory communities specifically due to differences in

topographic patterns, moisture and disturbance regimes, and land use histories between the two study areas. Therefore, forest communities containing an evergreen understory layer dominated by *K. latifolia* and/or *R. maximum* should be distinct compared to forest communities where an evergreen understory is not present, and these communities will vary from each other in their distribution in ordination space within and between the two study areas examined in this research.

2.2 Study Areas

The forest community affiliations and environmental gradient associations of the evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* were assessed in two study areas of the central Appalachian highlands that are representative of differing climatic regimes (Figure 1.3). One study area, encompassing the Green Ridge and Buchanan State Forests in Maryland and Pennsylvania, was located in the warmer and drier Ridge and Valley physiographic province, while the other is located on the cooler and wetter Allegheny Plateau (Savage River, Potomac, and Forbes State Forests in MD and PA). A considerable extent of these study areas has been designated as public forest or game lands, and thus experience less intensive development and logging pressure than adjacent private lands. Because of differences in topography and climate, as well as land use and disturbance history (Mash 1996), the composition and structure of forest communities in these two study areas are dissimilar from each other, but are representative of a broad range of environmental conditions typically found in the central Appalachian region.

2.2.1 Ridge and Valley Study Area

The Ridge and Valley study area is located in the oak-chestnut forest region designated by Braun (1950), and 92 out of the 108 plots (85 percent) established in this physiographic province have a canopy dominated by oak species. The Green Ridge State Forest (GRSF) area in Maryland was heavily cut for timber, tanbark, and hoop poles between 1879 and 1910, and wildfires were common in the regenerating forest for a number of years thereafter (Mash 1996). In the early and middle periods of the 20th century, much of the area that is now the GRSF was planted in fruit (primarily apple) orchards (Mash 1996). This intense land use history within the GRSF has influenced current forest composition, which is largely devoid of *K. latifolia* and *R. maximum* in the understory. The current forest of the Ridge and Valley study area is composed primarily of deciduous trees, mixed with a lesser amount of coniferous trees in the canopy. These forests are largely 50 to 75 years in age (CFI, unpublished data), with an average harvest rotational cycle of 84.5 years during the period of 1996 through 2001 based on the area cut per year from its 7,082 hectares under general management (online source; http://www.magicalliance.org/Forests/state_forest_harvest_plan.htm).

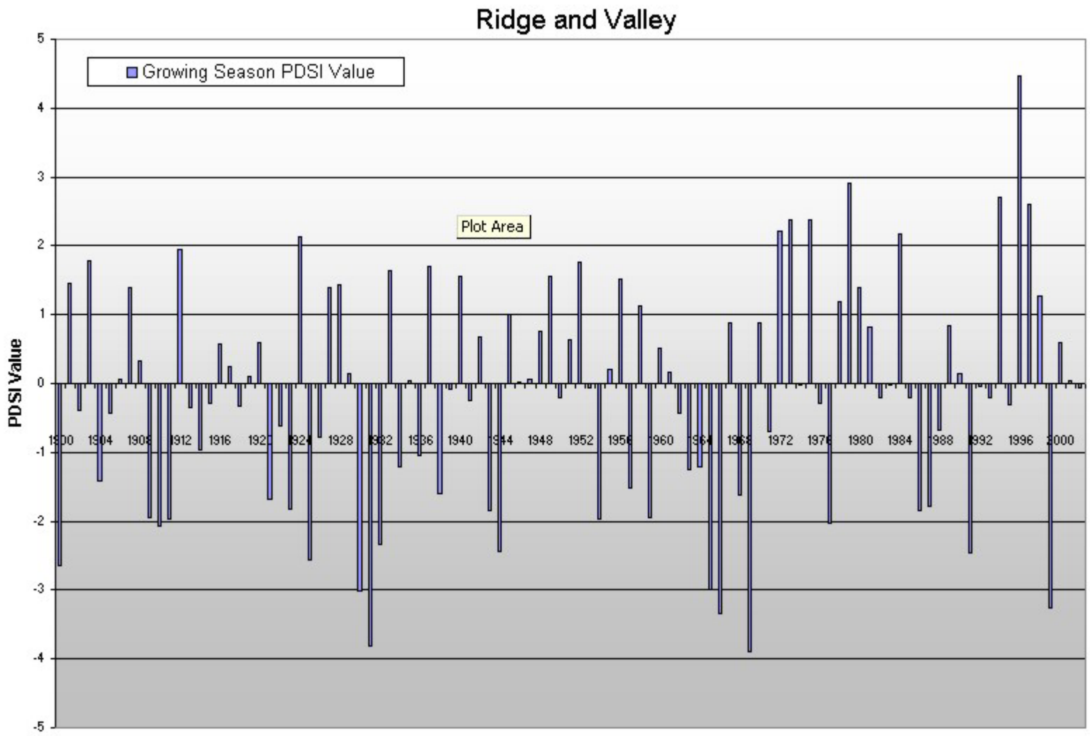
Field data from this research indicate that chestnut oak (*Quercus prinus*) ranks first in importance when relative basal area (RBA), amount of cover, and relative frequency are summed (Table A1). Red oak (*Quercus rubra*) is ranked second in importance, followed by white oak (*Quercus alba*) and scarlet oak (*Quercus coccinea*) (data from this research). Although black oak (*Quercus velutina*), Virginia pine (*Pinus virginiana*), and black gum (*Nyssa sylvatica*) are more dominant with respect to their RBA, red maple (*Acer rubrum*) occurs more frequently, and is thus the fifth highest in overall ranked importance in the Ridge and Valley physiographic province. In general, the data collected for this study can be considered geographically representative based on a comparison with RBA and relative frequency rankings from the Maryland continuous forest inventory (CFI) of 438 plots in GRSF. Some differences between these data and CFI were noted however. For example, *Q. alba* was the most commonly encountered and dominant tree species and *P. virginiana* was much more dominant and frequent in the CFI data. Some of the differences in these data sets may be due to the systematic nature of the CFI plot locations compared to the purposive sampling design of the data developed for this research (i.e. a portion of these plots deliberately located in evergreen understory areas). Also, the CFI plots were geographically limited to the boundaries of the GRSF.

Yearly average minimum and maximum temperatures for the GRSF were 2.3 and 15.8°C, with temperatures rarely exceeding 32°C in the summer months, but regularly dipping below -10°C in the winter (Stone and Matthews 1974). Elevation ranges from 123 to 845 meters, with steep northeast-southwest trending ridges in the GRSF and a larger contiguous upland area in the Martin Hill section of the Buchanan State Forest (BSF) in Pennsylvania. The annual precipitation range was 896 – 1297 mm (averaging 1023 mm) between 1983 and 1998 (Lynch, pers. comm.). Severe drought (as defined by an average Palmer Drought Severity Index (PDSI) value of –

3.0 or lower over the growing season months of April through September) has occurred five times between 1900 and 2002 in the Ridge and Valley study area: 1930, 1931, 1966, 1969, and 1999 (Figure 2.1). Mild to moderate drought (PDSI ranging from -1.50 to -2.99) has occurred 20 times since 1900, most recently in 1968, 1977, 1986, 1987, and 1991. Four major waves of gypsy moth infestation have occurred in this study area: the first in 1983-1984, another peaking in 1987, in 1990-1991, and finally in 2000-2001.

2.2.2 Allegheny Plateau Study Area

The Allegheny Plateau study area is considered part of the mixed mesophytic forest by Braun (1950). As with the Ridge and Valley, this area was largely cut in the 20th century, but much of the forest has been allowed to regenerate naturally in the interim, with an average harvest rotational cycle of 66.9 years in 1996 through 2001 based on the area cut per year of its approximately 11,736 hectares under general management (http://www.dnr.state.md.us/publiclands/savageplan04.html). The forest canopy in this study area was dominated by oak species in 80 out of 105 plots (76 percent) with localized areas dominated by eastern hemlock (*Tsuga canadensis*) and other conifers (*Pinus resinosa*, *Pinus strobus*, *Picea abies*, *Larix laricina*, and *Pinus sylvestris*) established in plantations during the 1940s following state acquisition of this area. Field survey data indicate that red oak (*Quercus rubra*) ranks first in overall importance (sum of RBA, amount of cover, and relative frequency), followed by red maple (*Acer rubrum*), chestnut oak (*Quercus prinus*), mountain laurel (*K. latifolia*), and white oak (*Quercus alba*) (Table A2). Hemlock is ranked fifth in RBA among all species sampled, but is ranked ninth in overall importance in the Allegheny



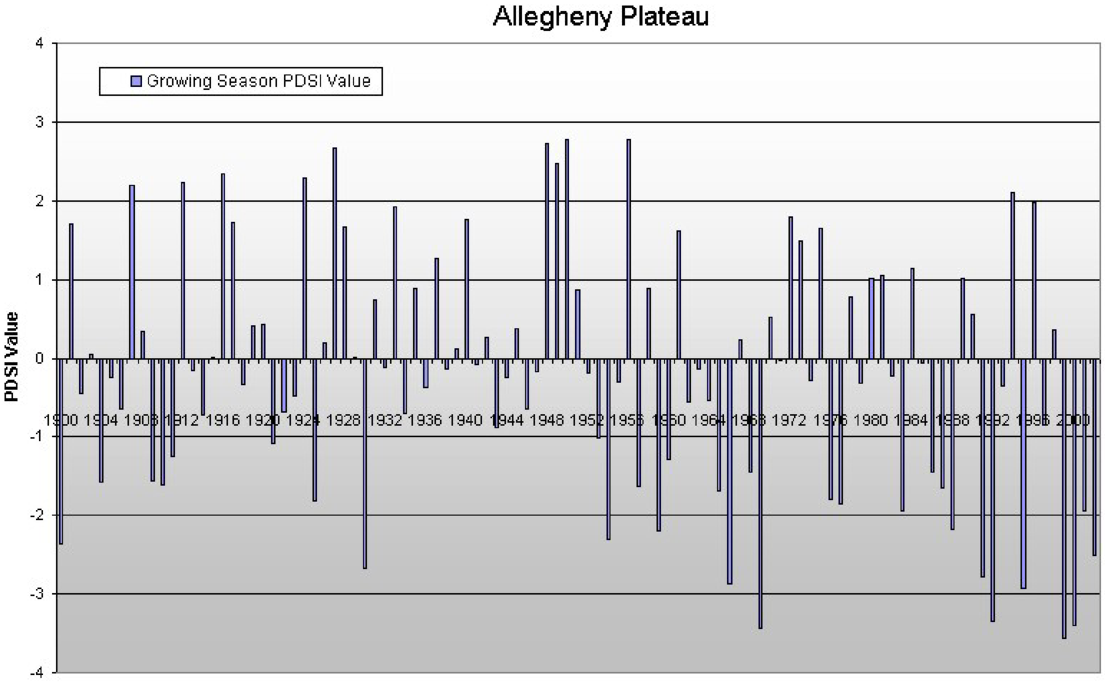


Figure 2.1: Bar charts showing the timing and severity of periodic drought in the Ridge and Valley and Allegheny Plateau provinces since 1900. Positive values of the Palmer Drought Severity Index (PDSI) indicate favorable hydrological conditions for plant growth (water surplus), while negative values indicate mild to moderate drought (-1.5 to –2.99) or severe drought (<-3.0).

Plateau study area because its relative frequency only ranked 12th among all species. American chestnut was an important component of these forests previous to its extirpation in the early to mid 20th century by the fungus *Cryphonectria parasitica* (Braun 1950), but is still ranked 17th in overall importance among all species found in this study area due to the high occurrence frequency of young or resprouted individuals. The data collected from 366 CFI plots in the SRSF are in general agreement with the data collected from this research, except that both black gum and sassafras were less frequent and dominant in the CFI data. This discrepancy is likely an artifact of the sampling design in this research, in which a portion of the plots were intentionally located in evergreen understory areas, where these two species often co-occur. Also, black oak is apparently underrepresented in the data collected for this research compared to its RBA and frequency ranks in the CFI data.

The elevation range for the Allegheny Plateau study area is 304-986 meters, with a humid continental climate characterized by severe winters and mild summers. The annual precipitation range between 1983 and 1998 was 913 – 1490 mm, with an average of 1216 mm (Lynch, pers. comm.). Severe drought (average growing season PDSI lower than -3.0) occurred four times since 1900 in the Allegheny Plateau study area; in 1969, 1992, 1999, and 2000. Mild to moderate drought (PDSI ranging from –1.50 to -2.99) has occurred 20 times since 1900, most recently in 1976, 1977, 1983, 1987, 1988, 1991, 1995, 2000, and 2001. Figure 2.1 illustrates the fluctuations in growing season water availability as represented by PDSI averages for the Allegheny

Plateau. Two major waves of gypsy moth infestation have occurred in this study area: The first in 1986-1987 and the second in 1990-1991.

2.3 Methods

2.3.1 Vegetation Sampling Design

Vegetation composition and structure data were obtained from 213 vegetation plots surveyed between 1999 and 2002, with 105 plots located on the Allegheny Plateau and 108 in the Ridge and Valley province. Of the 105 plots located in the Allegheny Plateau study area, 50 were located in 10 predetermined 10 hectare plots in SRSF within which bird surveys were conducted in 1999 and 2000, and an additional 25 plots were established in randomly chosen locations. In 2001, a total of 30 plots were purposely located in the SRSF in areas where an evergreen understory was present. Because some of the initial 75 plots established in 1999 and 2000 were located in forests which contained an evergreen understory component, a total of 61 evergreen understory plots were surveyed in the Allegheny Plateau province. Of the 108 plots located in the Ridge and Valley province, 60 were located in 12 predetermined 10 hectare plots in GRSF within which bird surveys were conducted in 1999 and 2000, and an additional 18 plots were located in other randomly chosen locations in GRSF. In 2002, a total of 30 plots were purposely located within the GRSF (Maryland), BSF (Pennsylvania), and other public lands in areas where an evergreen understory layer was present.

The layout of the 213 plots followed the design described by Townsend and Walsh (2001), with two crossing 60 meter transect tapes and five sample points located at the end of the transects and at their intersection (Figure 2.2). The orientation of the first transect line was pre-determined randomly. This plot design was chosen because it has the dual utility of efficiently characterizing forest composition while also being favorable for remote sensing studies (Grosenbaugh 1952, Lindsey *et al*. 1958, Justice and Townshend 1981, Townsend and Walsh 2001). The measurements made at these field survey plots included (Table A3): Basal area (BA) estimated at each of the sample points using a metric factor-2 Bitterlich prism; tree height measures (top and bottom of leaf canopy) taken for three canopy and three midstory trees at each sample point using a laser rangefinder; heights (top and bottom of leaf canopy) for all shrub/sapling species present with greater than 15 percent coverage; categorical cover estimates for the canopy, subcanopy, shrub/sapling, and herb layers as a whole and by species; leaf area index (LAI) at each plot using hemispherical photography acquired just above the height of the evergreen understory vegetation where present and at a height of 1 meter where no evergreen understory was present.

Because of the linear nature of some evergreen understory patches (i.e. along streams or ridges) and logistical concerns, plots representing the evergreen understory were limited to one 60 meter transect with three sample points - one at each end and one in the middle. So that all data points were consistent and all analyses were comparable, plots having two perpendicular transects were analyzed using only one randomly-selected transect (Figure 2.2).

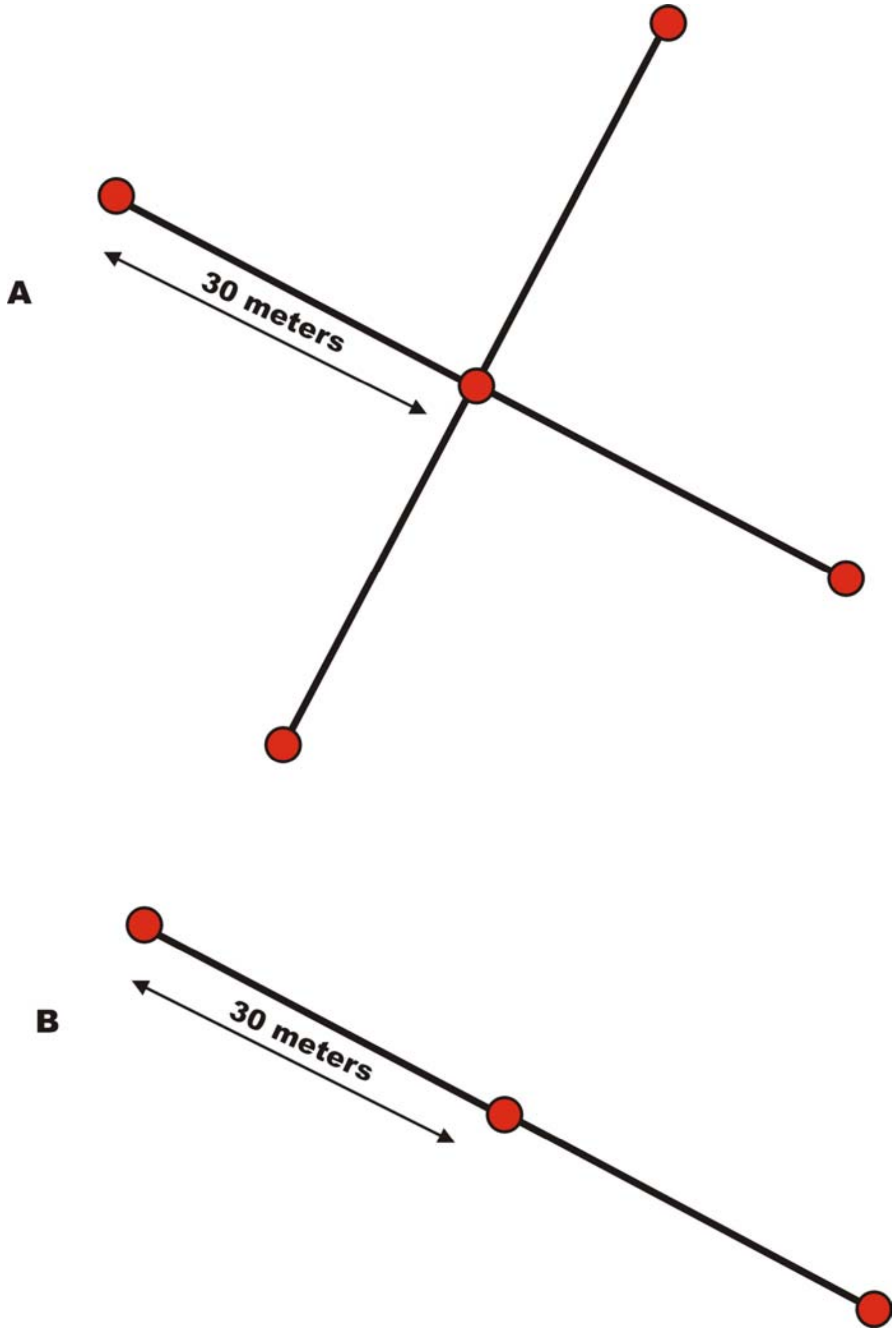


Figure 2.2: Designs for the original vegetation survey plots consisting of two intersecting 60 meter transects with five subplots (A) and the abridged evergreen understory plots consisting of only one single 60 meter transect with three subplots (B). The measurements taken at these plots are listed in Table A3.

2.3.2 Forest Community Classification

A cluster analysis using Ward's minimum variance method (Lance and Williams 1967) was performed to distinguish discrete forest vegetation classes (communities) in the vegetation survey data. Dissimilarity among plots was computed using the Sorenson statistic (Bray and Curtis 1957) based on an relative dominance value, which was calculated as a sum of the RBA and percent coverage of the individual species within each plot. The relative dominance was used to positively weight the evergreen understory shrub species whose BA was often low when computed using the Bitterlich variable plot method. Ward's method was then implemented in the SAS statistical software, producing an agglomerative hierarchical classification that could be used to distinguish groups of plots based on their floristic composition both in the canopy and understory strata. Specifically, it was possible to separate out classes for use in subsequent analyses of understory dominance by *K. latifolia*, *R. maximum*, or a combination of both.

2.3.3 Ordination

Nonmetric multidimensional scaling (NMS) ordination was performed using the software PC-Ord version 4.14 (McCune and Mefford 1999) on the relative dominance scores obtained for all species measured on the 213 plots. Ordination arranges species and samples along one or more dimensions so that similar species and samples are closer together and dissimilar ones are farther apart (Jongman *et al.* 1995). Ordination is often used as a data reduction technique to describe the strongest patterns or gradients of species composition using composite (synthetic) variables that comprise the majority of the variation in the data set. Implicit to ordination is the idea that regular patterns of species co-occurrence exist, but, unlike discrete classification techniques, the data are retained in a continuous form. For this study, ordination was conducted using data from both study areas together and separately to determine the extent to which composition varied according to different gradients within each area.

Species are hypothesized to respond to a number of topographic, disturbance, or resource gradients (which can be considered to control the gradients of composition described by the ordination). Correlation and regression were used to relate ordination scores to environmental variables (Table A4); species abundance was not used because of the large number of zero values typically found in vegetation data. In addition to topographic variables, the average annual precipitation (cm) between 1983 and 1998 (Lynch, pers. comm.) at each vegetation plot, percent rock cover, and the number of gypsy moth defoliations were also examined. All environmental variables were derived from GIS data layers except rock cover, which was estimated during field visits.

2.3.4 Forest Structure (ANOVA)

One-way ANOVA was used in this research to test the hypothesis that forest structure is simplified by the presence of the evergreen understory layer. Specifically, this analysis is intended to determine whether there is less volume in the midstory layer in forests underlain by an evergreen understory layer in the forests of the Allegheny Plateau and Ridge and Valley study areas compared to forests where an evergreen understory layer is absent. This phenomenon has been observed the southern Appalachians, where such forest stands have been described as two-tiered, consisting of the tree canopy and shrub layer, and this has been attributed to the inhibition of tree regeneration by evergreen understory layer vegetation. (Baker 1994, Hedman and Van Lear 1995, Baker and Van Lear 1998, Vandermast and Van Lear 2002). The volume of the midstory was reconstructed geometrically using the average depth of the vegetative matter in three midstory individuals on each of the three sample points per plot and determining coverage of the midstory layer from the percent coverage data estimated at each plot. This method was followed for each stratum to construct a simple model of forest structure for each plot in which the canopy, midstory, and understory layers are represented by volumetric shapes (Figure 2.3). Foliar volumes for the midstory and understory strata were calculated by representing their cross sectional area as an oval using the expression;

$$\int_0^H 15\sin(\pi / H)x$$

where H is the average height of the strata observed in the vegetation survey plots. The canopy stratum was represented as a more complex shape to avoid overestimation of its volume. The top 40 percent of its cross section was represented in a manner similar to the mid- and understory layers using the expression;

$$2\int_0^{0.4H} 15\cos(\pi / 0.4H)x$$

whereas the bottom 60 percent of the canopy strata cross section was represented using the expression for a gaussian curve:

$$2\int_0^{0.6H} 15e\text{-}(x^2/0.6*2H)$$

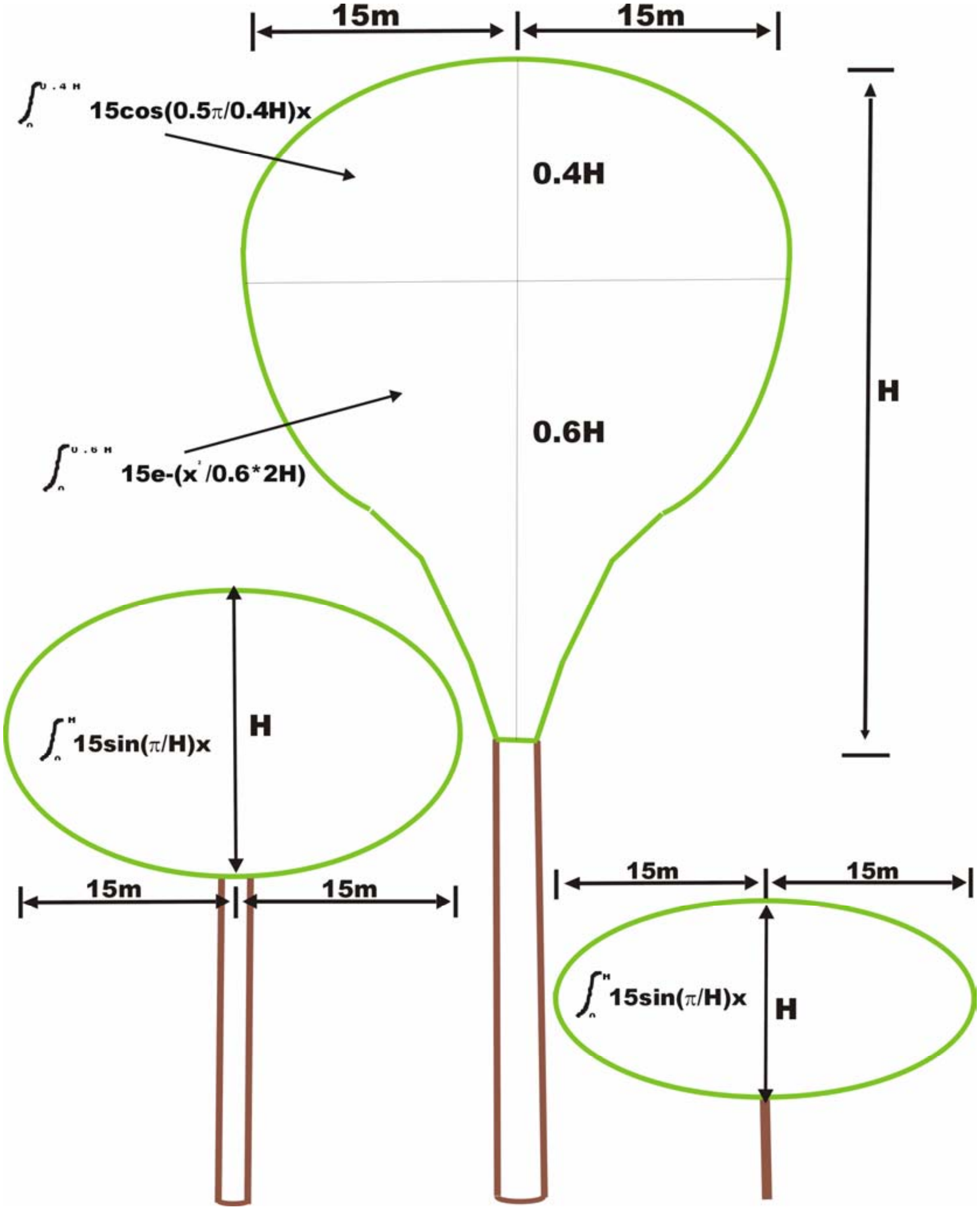


Figure 2.3: Schematic drawing of the simplified three-strata model of forest structure as developed for this research. These two-dimensional cross sectional depiction of canopy, midstory and understory layer vegetation were multiplied by the observed fractional percentage of coverage of a 30 meter cell so that the resulting volumes represent the cubic meters of volume that the individual strata would occupy in the 900 square meter areal footprint of a Landsat TM pixel. The canopy layer shape is split into four quadrants to indicate that the two mathematical expressions shown must be doubled then added together to represent the entire cross sectional area of this stratum.

thus allowing the bottom of the idealized shape of the canopy stratum cross-section to taper off similar to the typical shape of a forest tree. These cross-sectional areas (representing a 30 meter horizontal *x* dimension) were multiplied with the percent cover observed in each stratum in the vegetation survey plots, thereby incorporating that percentage as a proportion of a 30 meter cell *y* dimension to define a volumetric proportion of a hypothetical 30x30 meter (900 square meter) Landsat pixel for the canopy, subcanopy, and shrub/sapling strata. This areal entity was chosen to express strata volume so that it can later be incorporated with Landsat TM data in other portions of this research. Similarly, one-way ANOVA was used to examine the relationships between the presence of *K. latifolia* or *R. maximum* and BA and LAI in plots located in these two central Appalachian study areas. These two analyses were conducted to determine if *K. latifolia* understory communities were found in potentially poorer sites characterized by more open canopies (Wilson and O'Keefe 1983).

An additional one-way ANOVA was conducted to determine whether topographic factors, and not the presence or absence of an evergreen understory, were responsible for differences in forest structural attributes tested in this research. Specifically, because *K. latifolia* usually inhabits poor sites (Thomas and Grigal 1976, Wilson and O'Keefe 1983), one-way ANOVA was used to test whether the average topographic position of the plots where *K. latifolia* was present was significantly different than that of the 'control' (evergreen understory not present) and/or *R. maximum* plots examined in this study. Topographic position was represented for this comparison by the terrain relative moisture index (TRMI), which is an additive scale of site moisture potential (and hence site quality) based on the slope angle, aspect, position, and curvature of a location (Parker 1982). The result for the Ridge and Valley plots was not significant (df 2/103, F = 1.87, p = 0.165), with no significant difference among classed noted using Tukey's multiple comparison test. In the Allegheny Plateau, the one-way ANOVA result was significant (df 3/91, F = 3.23, p = 0.026), with the significant difference indicated by Tukey's multiple comparison test being that the *R. maximum* plots were moister than the 'control' plots. Because of these results, the one-way ANOVA tests for significant structural differences based on understory type proceeded under the assumption that topographic position was not a spurious factor.

Relationships among live basal area, LAI, and gypsy moth infestation were also examined to determine whether two decades of defoliation affected the current structural characteristics of the forest stands in the Ridge and Valley province. First, a two sample t-test was performed on 'control' (no evergreen understory) plots to test if LAI and BA differed significantly as a function of gypsy moth disturbance history. In addition, a two sample t-test was performed on *K. latifolia* and 'control' plots with a history of gypsy moth defoliation to examine if the presence of a *K. latifolia*-dominated understory significantly impacted overall forest structure (i.e. 'recovery' from disturbance). To control for topographic factors, separate two sample t-tests were conducted to determine if topographic moisture potential differed significantly between the defoliated 'control' plots and non-defoliated 'control' plots or between the defoliated *K. latifolia* plots and 'control' plots.

A final component to this study involved the examination of differences in *Acer rubrum* dominance between the forest canopy and the midstory. The objective was to determine the potential trajectory of forest change in ‘control’ and evergreen understory plots, especially because it has been observed that *A. rubrum* has increased in importance at the expense of various *Quercus* species as a consequence of fire suppression (Abrams 1992, 2003, Shumway *et al*. 2001). The comparison was conducted by tallying species that were selected for height measurements in the canopy and midstory strata. A total of 3 trees per stratum were randomly selected in each of three subplots, so that a total of 18 trees were measured within each plot (Figure 2.2, Table A3). From this sample, a comparative abundance of individuals was obtained.

2.4 Results and Discussion

2.4.1 Forest Community Classification

The clustering analysis identified nine major discrete groupings (Table 2.1) based on species associations, and 15 of discrete subgroup types based on variations in dominant and overstory species (Figure 2.4). Oak species were dominant or co-dominant in the canopy in 172 out of the 213 plots (81 percent). The 22 plots that were classified as ‘dry oak‘ (containing Q. *coccinea* and *Q. velutina*) all occurred in the Ridge and Valley province. A total of 80 evergreen understory plots were classified from the plot data, with 29 in the Ridge and Valley, and 51 in the

Table 2.1: Vegetation communities identified from the hierarchical forest community classification.

Group	Type	Number of Plots Total	 Ridge/Valley	 Plateau
Oak Forests	chestnut oak dominated	22	17	5
	white oak dominated	8	8	0
	red oak dominated	3	0	3
	mixed oak	20	13	7
Dry Oak Forests		22	22	0
Red Maple/Oak Forests	red maple with red oak	19	6	13
	red maple with chestnut oak	8	0	8
Conifer Forests		6	6	0
Sugar Maple Forests		21	7	14
Kalmia Understory Forests	Kalmia with chestnut oak canopy	37	26	11
	Kalmia with maple-oak canopy	18	0	18
	Kalmia with red oak canopy	4	0	4
Mixed (Kalmia and Rhododendron) Understory Forests	Mixed understory with maple/oak canopy	11	0	11
Rhododendron Understory Forests		10	3	7
Hemlock Forests		4	0	4
	Total Plots	213	108	105
	Evergreen Understory Plots	80	29	51

Allegheny Plateau study area. These community classifications were used in subsequent analysis to assess their separability in ordination species-space. The schematic dendrogram shown in Figure 2.4 indicates that the vegetation plot data sorted out into community types to some extent according to edaphic characteristics, with more mesic communities such as those containing a *R. maximum* understory or a sugar maple or hemlock canopy separating out from the same 'branches'. Also, the community types containing a *K latifolia*-dominated understory originated from the same dendrogram branch.

2.4.2 Ordination Results

NMS ordination showed clear separation between the two study areas, among species assemblages, and the discrete vegetation groupings identified through cluster analysis (Figures 2.5 – 2.7). In addition, joint plots with the environmental variables, where the length and direction of the environmental vector are scaled to the strength and direction of the correlation of that variable with the ordination axes, indicate readily interpretable relationships between species and environmental gradients. Using all plots in both study areas, ordination scores exhibited a cumulative coefficient of determination of .821 with the original distances in the species matrix, indicating that the ordination effectively characterized the original data set (Table A5). Ridge and Valley and Plateau plots were distinct from each other in species-space in the NMS joint plot (Figure 2.5), indicating clear differences in species assemblages between the two physiographic provinces. The amount of precipitation and height in elevation increased in the direction of the Plateau plots, indicating the cooler and wetter

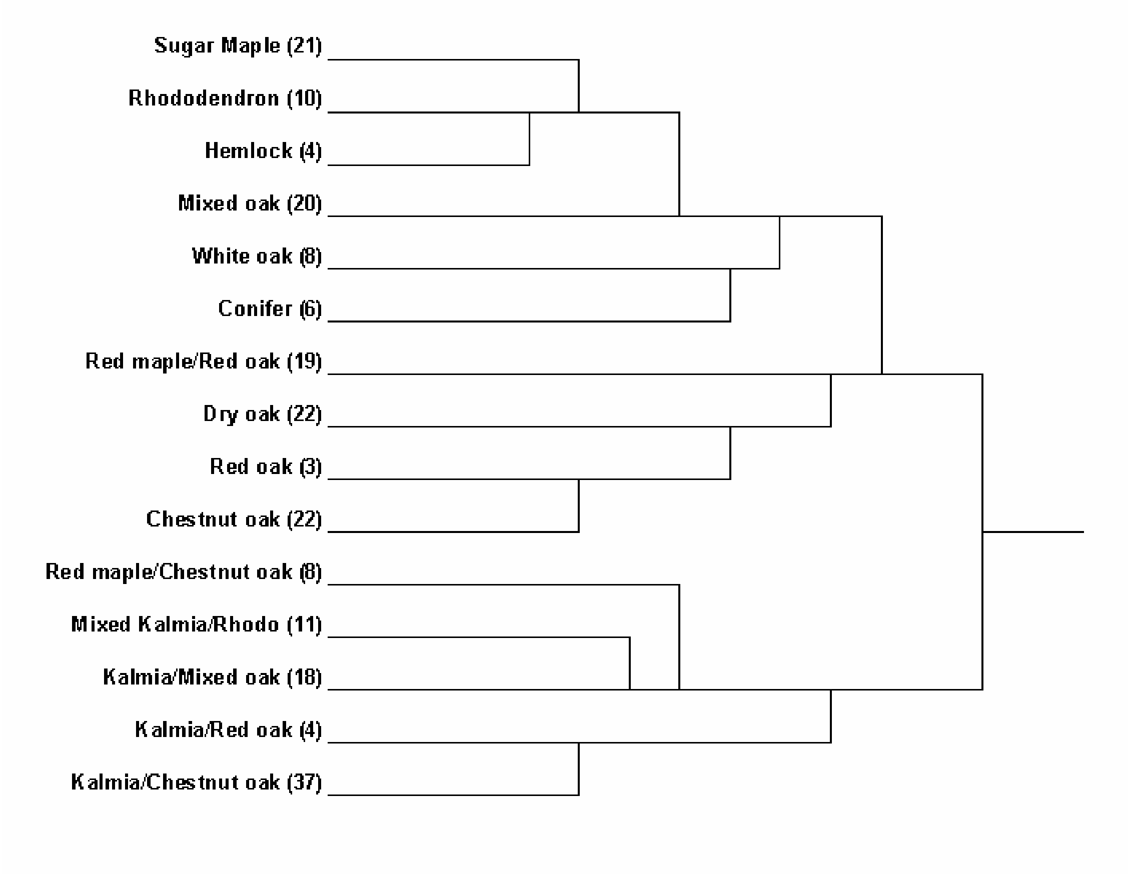


Figure 2.4: Dendrogram illustrating the results of the cluster analysis of vegetation plot data from the Ridge and Valley and Allegheny Plateau study areas. The number of plots in each of the classes are noted parenthetically.

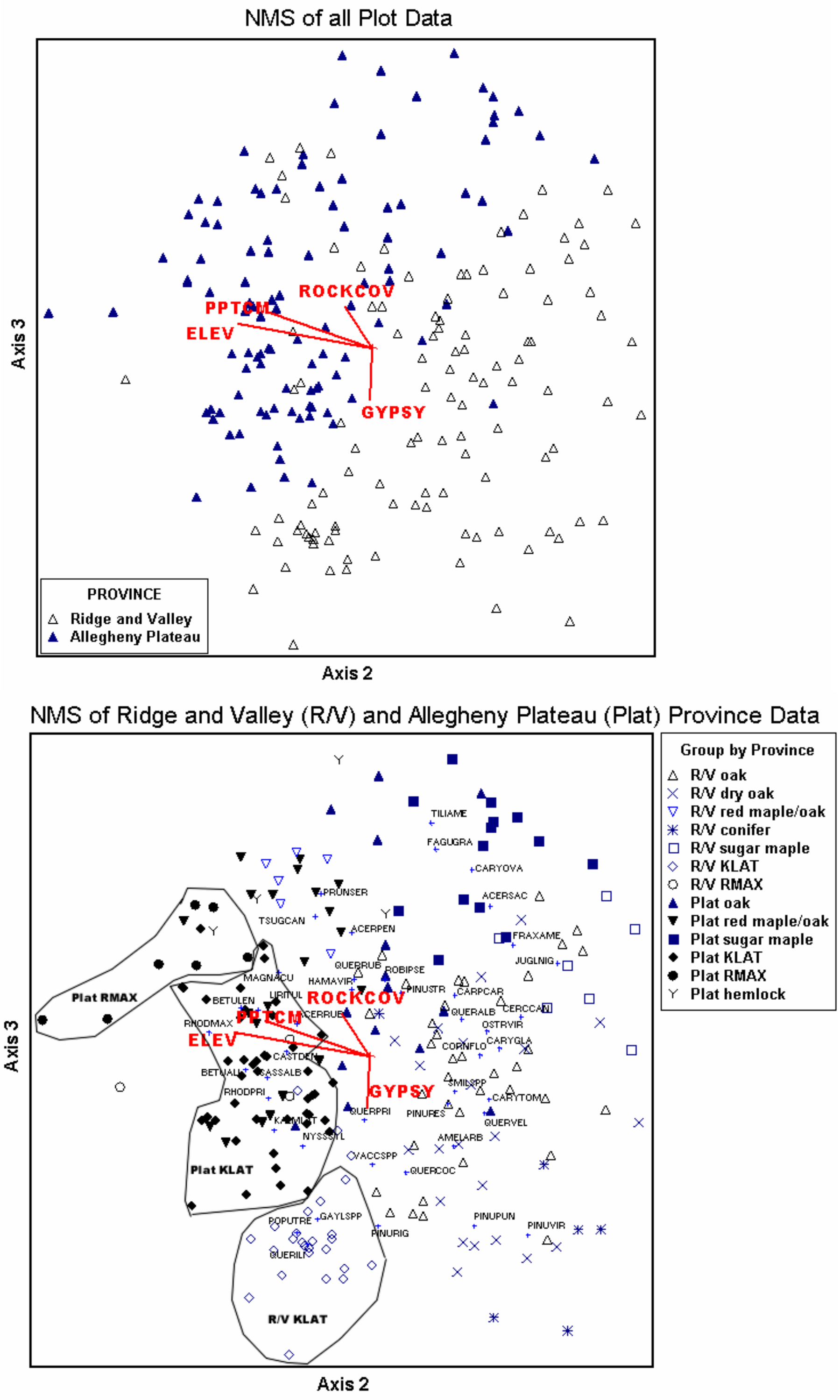


Figure 2.5: Joint plots of the results of an NMS ordination of species relative dominance scores and environmental variables from all 213 plots located across both study areas delineated for this research. The top joint plot illustrates the separation between the two physiographic provinces, while the bottom one highlights the separability of the different evergreen understory community types (*K. latifolia* = KLAT and *R. maximum* = RMAX) within and between the two study areas.

climatic regime in the Plateau compared to the Ridge and Valley province (Figure 2.5, Table A5). In addition, the increase in rock cover in the direction of the Allegheny Plateau plots can be viewed as a surrogate indicator of a less intensive land use history the Plateau compared to the Ridge and Valley province (i.e. in the GRSF area, see Mash 1996). Finally, *K. latifolia*- and *R. maximum*-dominated plots are separate from other vegetation types and each other in the ordination of all of the plot data from the two provinces. Notably, the Ridge and Valley *K. latifolia* plots and the Plateau *K. latifolia* plots are distinct from each other on this plot, with *K. latifolia* presence strongly related to the amount of gypsy moth defoliation in the Ridge and Valley. Also, it is apparent that bear oak (*Quercus ilicifolia*) was associated with the gypsy moth disturbed *K. latifolia* understory communities in the Ridge and Valley province, whereas early azalea (*Rhododendron prinophyllum*) and sassafras (*sassafras albidum*) are more associated with ericaceous *K. latifolia* communities in the Plateau province.

In the ordination of data obtained from the Ridge and Valley alone (Figure 2.6, Table A6), *K. latifolia* dominance appears strongly related to the gypsy moth disturbance gradient (r with ordination axis 1 = -0.57). In addition, all 3 of the *R. maximum* plots are located together, but separate from the rest of the plots, with the elevation gradient strongly related to them (r with ordination axis 3 = -0.62). It is assumed that the relationship between the *R. maximum* plots and the elevation gradient is related to the absence of *R. maximum* at many lower elevation locations in the portion of the Ridge and Valley study area located in southern Pennsylvania due to the tendency for valley

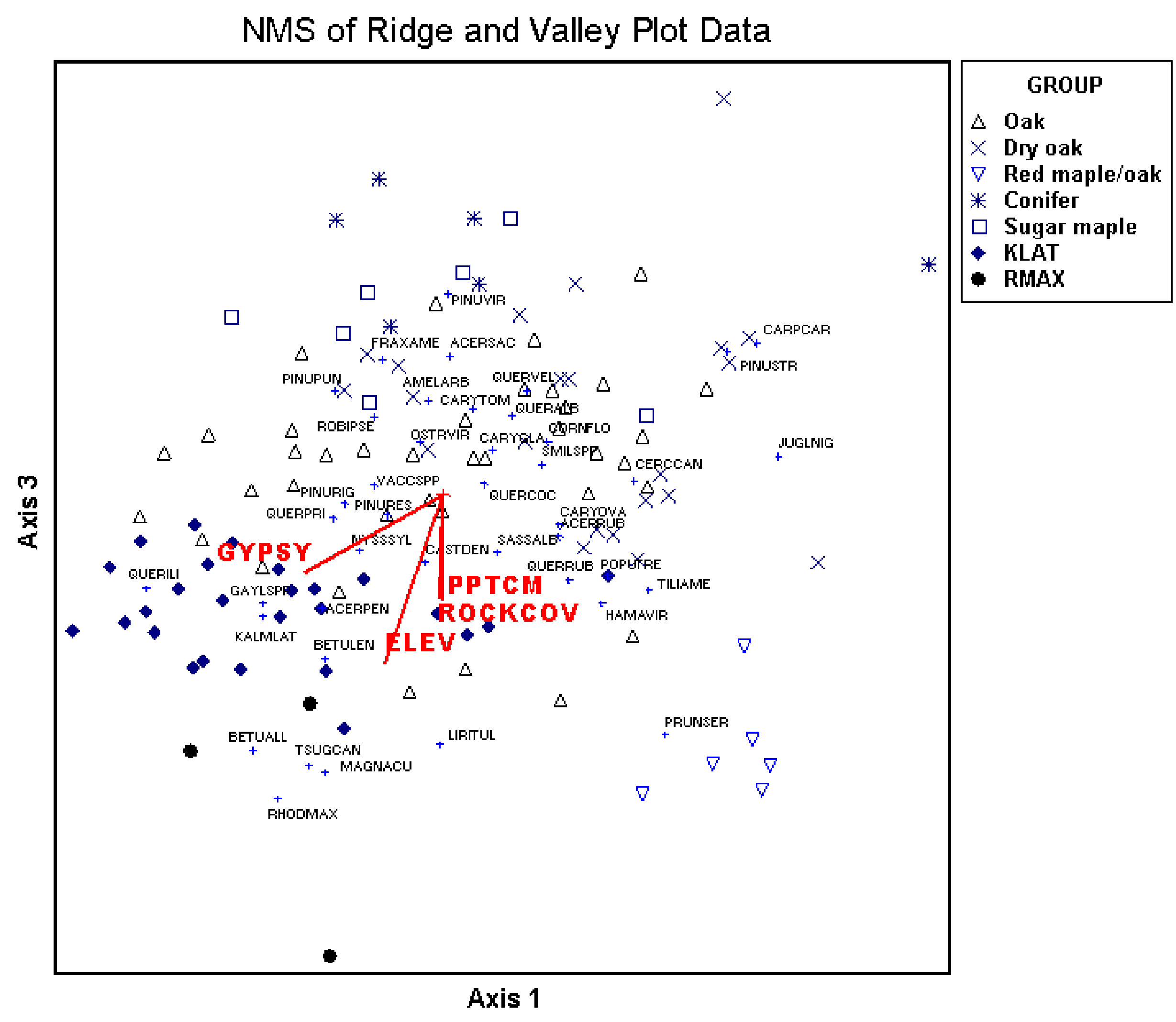


Figure 2.6: Joint plot of the results of an NMS ordination of species relative dominance scores and environmental variables from the Ridge and Valley vegetation plot data. Note the relationship between the location of the *K. latifolia* plots and gypsy moth infestation disturbance gradient.

bottoms in this region to be underlain with limestone or dolomite (Romancier 1970). Also, the rock cover gradient is negatively related (r with ordination axis 3 = -0.49) to the *P. virginiana* dominated conifer plots in GRSF, supporting the assumption that these are former agricultural areas (Mash 1996).

The NMS ordination of the SRSF plot data alone suggests the overall importance of topographic gradients on the Allegheny Plateau (Figure 2.7), as the history of gypsy moth disturbance and land use is less intense. The TCI (wetness index) gradient increases in the direction of the plots containing the moisture-loving *R. maximum*, and the slope gradient decreases in that direction. Pearson correlations for TCI with ordination axis 1 = -0.42 and for Slope with axis 1 = 0.38 (Table A7). Similarly, LFI (a gradient of exposed to protected sites) decreases and elevation increases in the direction of the drier *K. latifolia* plots. Pearson correlations for LFI with axis 2 = 0.44 and for elevation with axis 2 = -0.46.

2.4.3 Results from Analysis of Forest Structural Features

The results of a one-way ANOVA indicated that the presence of an evergreen understory was significantly related to a smaller midstory layer volume in some, but not all understory types in the two study areas (Figure 2.8). In the Ridge and Valley province, one-way ANOVA results indicated a significant difference in midstory volume by plot type (df 2/103, F = 16.75, p < .0001), but whereas Tukey's multiple comparison test revealed that *K. latifolia* plots had a significantly lower midstory volume than 'control' (no evergreen understory) plots, *R. maximum* sites were not

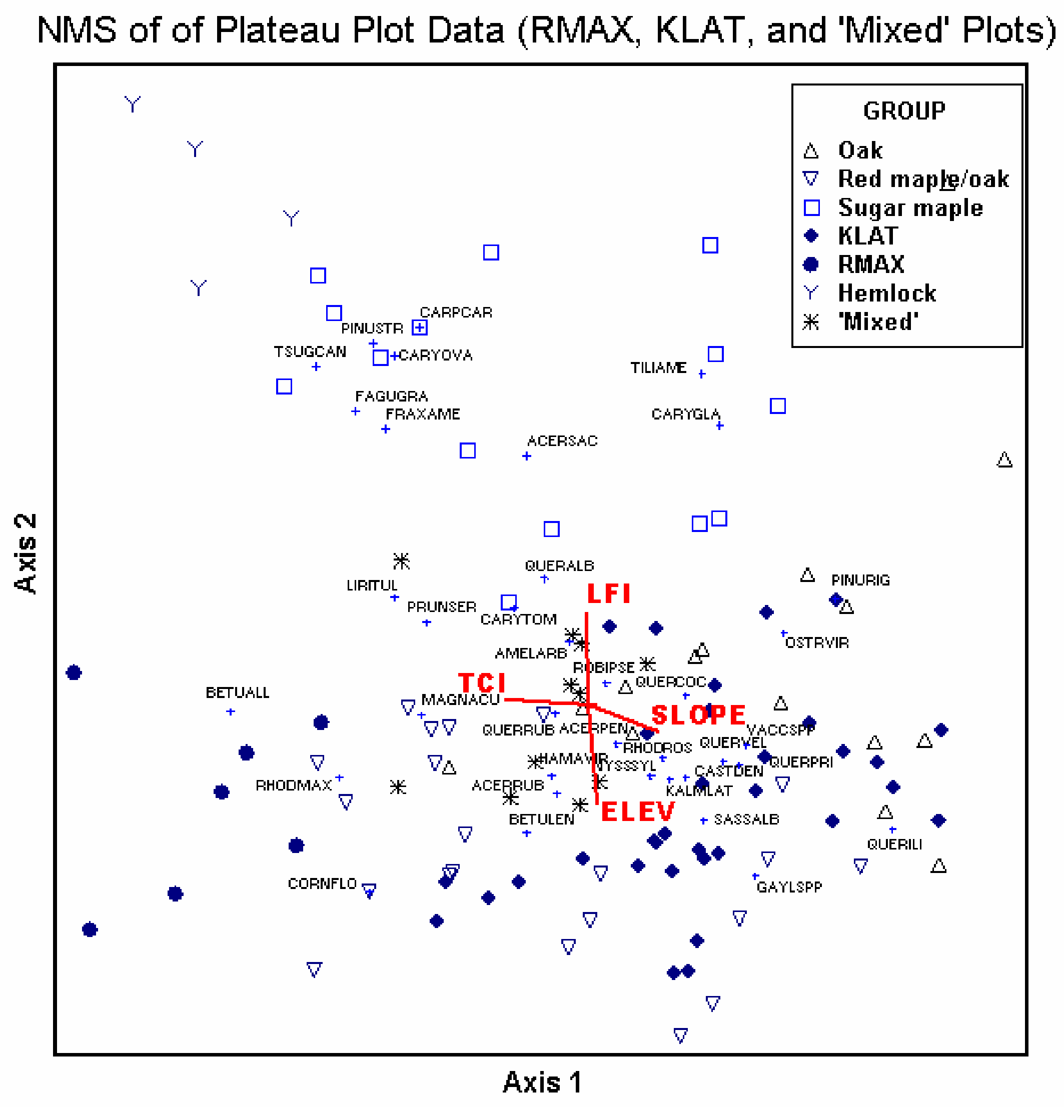


Figure 2.7: Joint plot of the results of an NMS ordination of species relative dominance scores and environmental variables from the Allegheny Plateau vegetation plot data showing the relationships between the topographic gradients and the evergreen understory plot types.

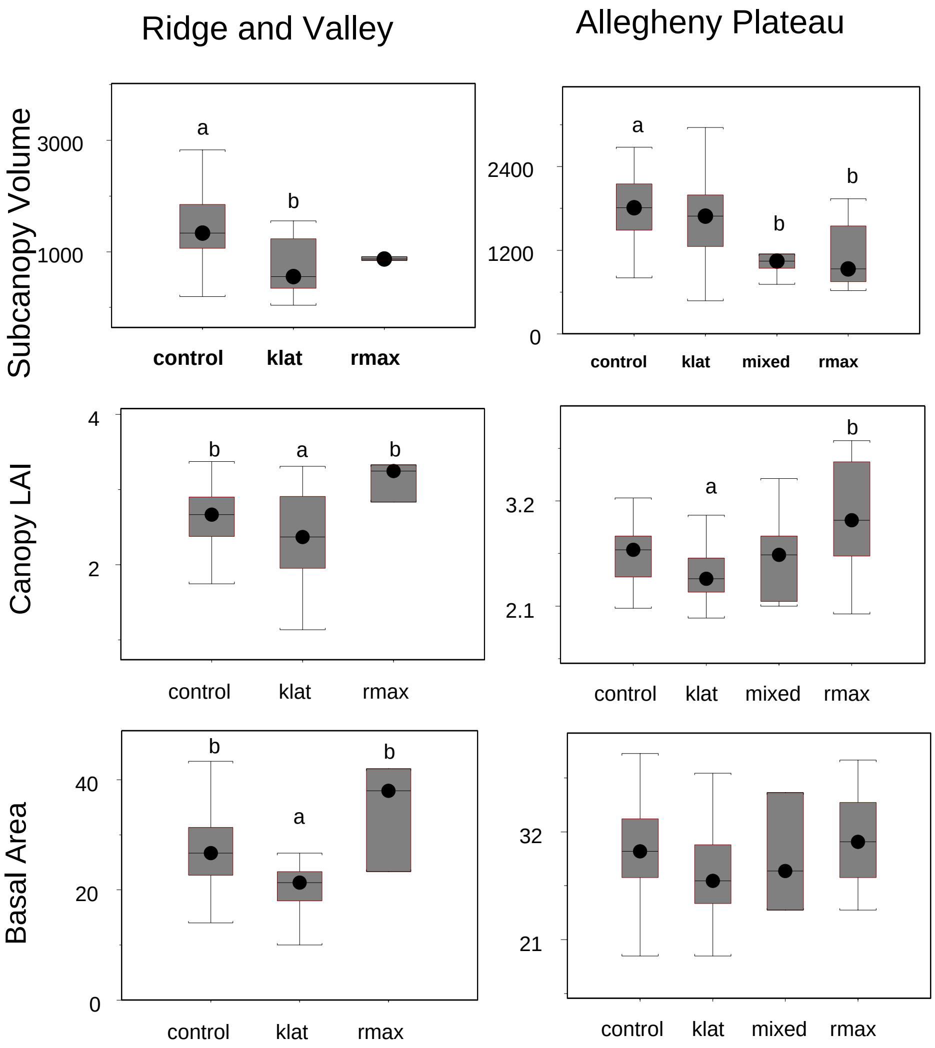


Figure 2.8: Box and whisker plots of subcanopy foliar volume, LAI above the understory layer, and basal area for the Allegheny Plateau and Ridge and Valley study areas. The y-axis value for subcanopy foliar volume is a relative measure of cubic meters per 900 meters square, which is the area of a 30-m Landsat TM pixel. The ‘control’ class refers to plots where an evergreen understory was not present, whereas ‘klat’ refers to *K. latifolia* plots and ‘rmax’ refers to *R. maximum* plots. Different letters indicate significant differences in classes shown in charts, while unlettered boxes indicate the lack of significant differences detected using Tukey’s multiple comparison test.

significantly different from either the *K. latifolia* or 'control' plots. However, the *R. maximum* plots in this province were limited in spatial extent and concentrated in narrow riparian areas where patch width was so small as to preclude the gathering of a sufficient sample to adequately characterize the midstory layer for this study. One-way ANOVA also indicated that *K. latifolia* plots had significantly lower LAI compared to the 'control' and *R. maximum* plots in the Ridge and Valley province (df 2/103, F = 6.76, p = .0018). Further, live BA was significantly lower on *K. latifolia* plots compared to both the 'control' and *R. maximum* sites (df 2/103, F = 18.85, p < .0001). Therefore, the upper strata of the forest stands with a *K. latifolia*-dominated understory were demonstrably more open than is typical of other forest stand types in the Ridge and Valley area.

Results from the one-way ANOVA on the Allegheny Plateau indicated that the midstory volume of the mixed and *R. maximum* plots was significantly lower than the midstory volume in the 'control' plots (df 3/91, F = 4.9, p = .0034). This result is bolstered by the previous finding that the Plateau *R. maximum* plots are significantly more mesic than the 'control' plots to which they were compared. Surprisingly, the *K. latifolia* plots and 'control' plots were not significantly different with respect to midstory volume (Figure 2.8). This lack of significance is related to the patchiness of *K. latifolia* communities located on the Plateau compared to those in the Ridge and Valley. Patchiness was computed as the ratio of stem counts between the two transect lines on the plots, with larger positive departures from a value of 1 indicative of increasing inequality. The average ratio for the Allegheny Plateau *K. latifolia* plots was higher (4.39) than the corresponding average for the Ridge and Valley *K. latifolia* plots (1.89), with a two-sample t-test indicating significant difference (p = .0404) between them. The one-way ANOVA results also indicated that Allegheny Plateau *K. latifolia* plots had a significantly lower average LAI than *R. maximum* plots (df 3/91, F = 5.64, p = .0014), but was not significantly lower than the average LAI on the 'control' plots. No significant differences in basal area were noted between the Plateau plot types.

The investigation into relationships among live basal area, LAI, and gypsy moth infestation indicated significant differences both as a function of defoliation history and *K. latifolia* presence versus absence. Not surprisingly, the results of a two sample t-test indicated that the BA and LAI were lower in 'control' plots with a gypsy moth infestation history compared to 'control' plots where no infestations had occurred. The difference was significant for BA (p = .0002), but not for LAI (p = .1273). Also, the mean values for LAI and BA were lower in the *K. latifolia* plots with a history of defoliation than they were for 'control' plots with a comparable disturbance history, but again the difference was significant only for BA (p = .0023), and not for LAI (p = .1201). All of the *K. latifolia* plots visited for this research have a history of gypsy moth infestations, so unfortunately a comparison of LAI and BA for *K. latifolia* plots as a function of this disturbance history cannot be performed with available data.

The results of the examination of the relative abundance of *Acer rubrum* in the forest canopy and the midstory indicated that *A. rubrum* is far more abundant in the midstory layer compared to the canopy layer in the forests of both study areas. In the Ridge and Valley province, there were 10 times as many red maple in the midstory compared to the canopy (Table 2.2). In the Allegheny Plateau province, *A. rubrum* was 2.56 times as plentiful. In both cases, this inequality was more pronounced in plots where there was no evergreen understory layer (‘control’ plots), most likely due to the seedling establishment difficulties present for all tree species under evergreen understory thickets (Clinton and Vose 1996). Although the selection process for tree height measurement does not constitute a formal research design to conclude that red maples are over-represented in the midstory layer based on these numbers, it provides further circumstantial evidence of changing forest regeneration trends in the Appalachians. As a point of reference, it was also found that there were many more oaks in the canopy (640) compared to the midstory (98) layer in the Plateau as well as in the Ridge and Valley study area (776 and 313, respectively). This result indicates that the vast majority of oak trees in the forests of both physiographic provinces (especially in the Allegheny Plateau) currently live in the canopy layer with comparatively fewer individuals in the midstory layer, and suggests that stand replacement will be maples rather than oaks in the absence of major stand removing disturbance regardless of understory type.

2.5 Conclusions

The composition and structure of forests in the central Appalachian highlands have developed as a result of climate, topography, land use, and disturbance. Disturbance and land use tend to complicate the association between vegetation patterns and the

Table 2.2: Numbers of red maple (*Acer rubrum*) and all varieties of oaks (*Quercus spp*.) chosen in the course of determining average heights in the canopy and subcanopy strata in the Ridge and Valley and Allegheny Plateau study area plots. The ratios represent a measure of the inequality between the two strata within the individual plot types.

Province	**Plot Type**	**Red Maples Measured**		**Ratio**
		Canopy	**Midstory**	**Midstory/Canopy**
Ridge and Valley	Kalmia	5	32	6.4
	Rhododendron	3	7	2.33
	Control	5	91	18.2
	All Plots	13	130	10
Allegheny Plateau	Kalmia	72	165	2.29
	Rhododendron	14	36	2.57
	Mixed	15	24	1.6
	Control	23	93	4.04
	All Plots	124	318	2.56

		Oaks Measured		**Ratio**
		Canopy	**Midstory**	**Midstory/Canopy**
Ridge and Valley	Kalmia	189	92	.49
	Rhododendron	10	2	.20
	Control	577	219	.38
	All Plots	776	313	.40
Allegheny Plateau	Kalmia	316	56	.18
	Rhododendron	32	6	.19
	Mixed	44	2	.05
	Control	248	34	.14
	All Plots	640	98	.15

direct and resource gradients that influence forest composition. Ordination analysis showed that the primary differences found in the forest composition data was related to climatic variations associated with physiographic setting (Figure 2.5). Indirect gradients related to topography (moisture and exposure gradients), disturbance (gypsy moth defoliation), and land use history (rock cover) were also important for explaining the within-province ordination space distribution of the forest communities, especially those containing *K. latifolia* and *R. maximum* (Figures 2.6 and 2.7). Distributions of evergreen understory communities in turn influence the structural characteristics of forest stands. In the Ridge and Valley, gypsy moth defoliation opens the subcanopy light environment permitting the development of dense and continuous stands of *Kalmia*. On the Allegheny Plateau, climate and terrain-related gradients distinguished *K. latifolia* and *R. maximum* from each other and forests without an evergreen understory layer, but the less intense gypsy moth disturbance regime may have played a role in the development of a patchier *K. latifolia* layer where it is found. Finally, the data indicate that the presence of an evergreen understory layer significantly simplifies the structural complexity of forest stands, contributing to a less well developed midstory layer. This phenomenon is interpreted as resulting from an inhibition of canopy tree regeneration, and points out the potential regional scale impact of the evergreen understory on the future compositional and structural attributes of central Appalachian forest communities.

The research presented here provides data and analysis to assess on a regional scale the spatial implications of understory communities on overall forest structure, stand dynamics, and regeneration. The study provided the plot-level analyses to demonstrate that there are tangible floristic and structural differences related to the presence of evergreen understory communities dominated by *K. latifolia*- and *R. maximum* in the forests located within the Ridge and Valley and Allegheny Plateau physiographic provinces of the central Appalachian Mountains. The next step involves mapping the spatial distribution of these evergreen understory communities across the two provinces using remote sensing data in conjunction with data on topographic gradients as developed here. Once the areal extent of these communities are known, an examination of the temporal dynamics of these communities using remote sensing data and dendrochronological methods can be undertaken to further evaluate the growth vigor variability of these species and assess their potential for long term inhibition of canopy tree regeneration. An assessment of the influence of these understory communities with respect to carbon sequestration and nutrient dynamics on a landscape scale can also be performed via simulation modeling using the known spatial extent of these evergreen understory communities. The ultimate research aim is to explore the prevalence, ecological impacts, and potential future influence of these evergreen understory communities to provide the basis for informed forest management decisions and adaptive management strategies.

Chapter 3: Use of Landsat Enhanced Thematic Mapper Imagery and Ancillary Information to Characterize Evergreen Understory Communities

Abstract

Evergreen understory vegetation was classified using Landsat imagery and ancillary data in two forested study areas in the central Appalachian highlands, one in the warmer and drier Ridge and Valley physiographic province and the other on the wetter and cooler Allegheny Plateau. The two study areas represent a range of conditions found in the Central Appalachians due to differences in topography, climate, and land use. The evergreen understory communities are dominated by rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.), which are spatially extensive and ecologically important to the structure and functioning of Appalachian forests. Ancillary information was integrated with remote sensing data to improve classification accuracy, and multiple classification strategies were tested for their utility. An overall accuracy of 87.1 percent was achieved in the Ridge and Valley study area, while an 82.9 percent overall accuracy was obtained for the Allegheny Plateau. Overall accuracy was improved in the Plateau region by incorporating topographic information into the classification process, but inclusion of topographic information increased confusion among winter-green vegetation types in the Ridge and Valley study area.

3.1 Intoduction

Society relies on forests to provide a number of economic and ecosystem services (Daily *et al*. 1997), requiring a balance between providing wood and other products with the maintenance of water quality, sediment retention, and the capacity for nutrient storage (Perry 1998, Aber et al. 2000). In addition, forests act as carbon sinks that can attenuate climatic changes due to increases in atmospheric carbon (Schlesinger 1977, Sedjo 1992, Currie et al. 2003). Forest ecosystems also provide habitat and refuge for wildlife, and are valued for recreation and aesthetics. Given these societal services, there is general agreement on the importance of forest ecosystems to be self-replacing and sustainable into the foreseeable future.

In the eastern United States, the Appalachian region contains the most extensive contiguous area of forests, because high topographic relief precludes their large scale transformation into agricultural or urban land uses. An important – but often understudied – component of Appalachian forests is the evergreen understory layer found beneath the canopy of large tracts of these forests. Appalachian evergreen understory communities are dominated by rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) in nearly pure stands or mixed in varying proportions. Their locations are correlated with topography, with *R. maximum* thriving in protected, mesic locations and *K. latifolia* often located on exposed, upslope sites (Figure 3.1). The different landscape positions inhabited by these two species result from differences in plant physiological responses to solar radiation, cold air drainage, soil moisture, summer and winter temperature regimes, and atmospheric drying potentials (Davidson 1966, Monk *et al.* 1985, Lipscomb and Nilsen 1990a, 1990b, Muller 1991, Dobbs 1995). The evergreen understory layer species *K. latifolia* and *R. maximum* are important to forest community structure and ecosystem function because they:

1) Have the potential for slowing mineral cycling (McGinty 1972, Thomas and Grigal 1976, Monk *et al.* 1985), and therefore have water quality maintenance

implications in the event of disturbance. *R. maximum* has been referred to as a keystone species in this regard (Yeakley *et al*. 1994);

2) Inhibit canopy tree regeneration when present in dense stands (Minkler 1941, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al.* 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002);
3) Provide forage and refuge for various wildlife (Gates and Harman 1980, Thackston *et al*. 1982, Johnson *et al*. 1995, Spear 1998);
4) Are significant with respect to carbon sequestration and nutrient (N and P) cycling (McGinty 1972, Thomas and Grigal 1976, Monk *et al*. 1985);
5) Enhance the aesthetics of Appalachian forests (Hollenhorst *et al*. 1993).

Further study of the evergreen understory species *K. latifolia* and *R. maximum* is needed because their spatial extent and temporal dynamics are poorly understood. Insight into to their temporal dynamics with respect to both leaf area (density) and spatial extent is key to understanding their role in the inhibition of canopy tree regeneration (McGee and Smith 1967). In addition, the spatial dynamics of *R. maximum* and *K. latifolia* provide the context to understand their role in carbon sequestration and mineral cycling on the landscape and regional scales, and subsequent role in water quality maintenance (McGinty 1972, Thomas and Grigal 1976, Monk *et al.* 1985, Yeakley *et al*. 1994). Accurate mapping of the current spatial extent of the *K. latifolia*- and *R. maximum*-dominated evergreen understory layer in the central Appalachian highlands will provide baseline data to examine the

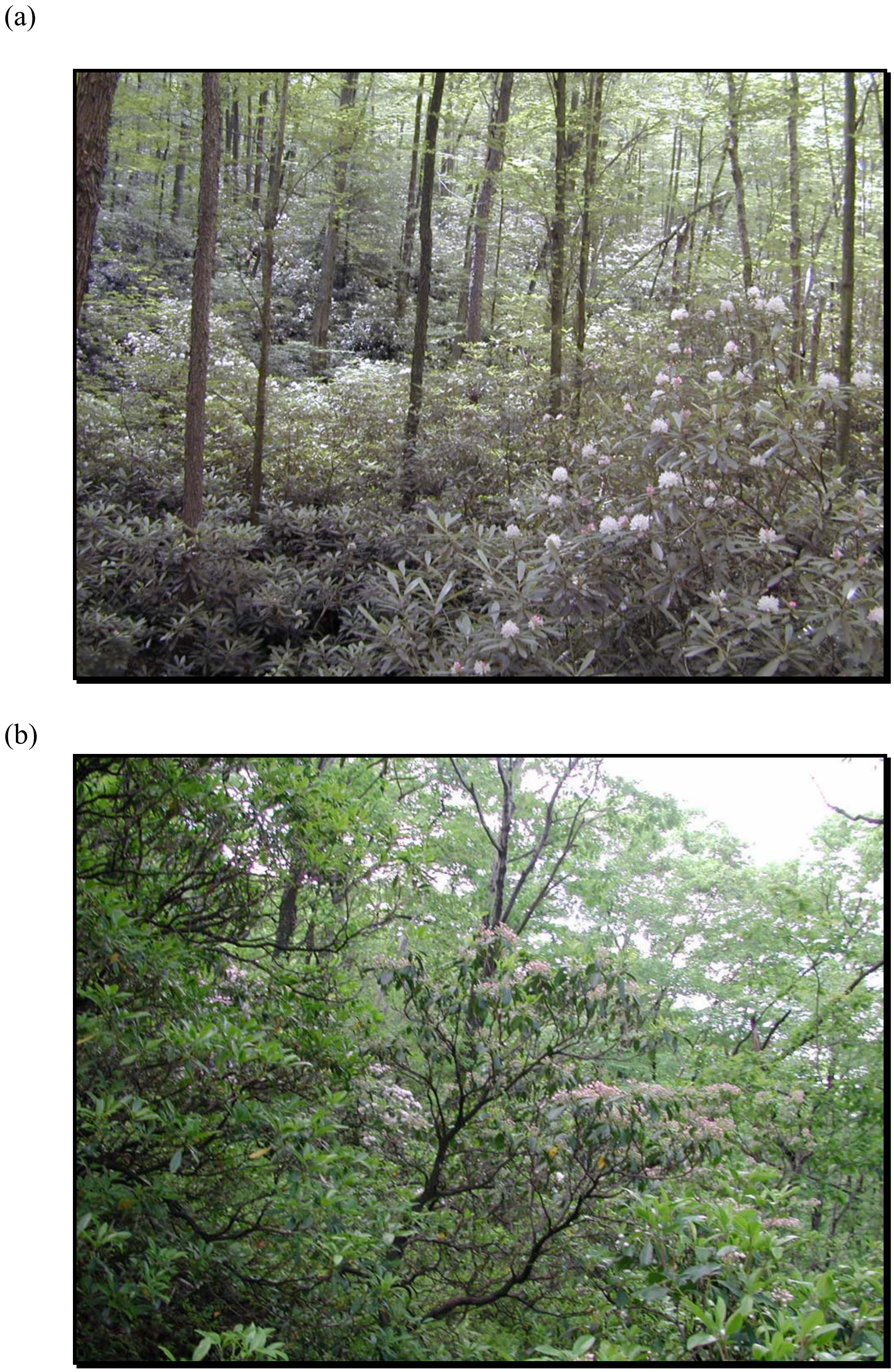


Figure 3.1: Examples of (a) a rhododendron-dominated evergreen understory community in a mesic, protected cove location and (b) a mountain laurel-dominated community on an exposed, upper slope location (near a ridge top).

total regional scale influence of evergreen understories on the inhibition of canopy regeneration and the potential for carbon sequestration by forests.

Evergreen understories that are dominated by *K. latifolia* and *R. maximum* have steadily increased during the 20th century in both spatial extent and density in Appalachian forests due to canopy tree disease, management practices, and other disturbances (Woods and Shank 1959, Smith 1963, Romancier 1970, Monk *et al*. 1985, Phillips and Murdy 1985, Baker 1994, Vandermast *et al*. 2002, Vandermast and Van Lear 2002). Some researchers have observed that the spatial extent of *R. maximum* is increasing in the southern Appalachians, but that the cover of *K. latifolia* has remained comparatively stable (Dobbs 1995). However, others have noted an increase in the area of dense stands of *K. latifolia* on xeric upper slope sites in the Southern Appalachians resulting from high-grading of pitch pines and insect outbreaks (Elliott *et al*. 1999, Waldrop *et al*. 2000). In the Central Appalachians, it has been observed that *R. maximum* is becoming increasingly important, with thickets located in more mesic areas becoming denser and those in drier areas showing evidence of spreading (Plocher and Carvell 1987, McGraw 1989), but this has not been substantiated on the landscape scale.

The presence of thickets of the evergreen shrub species *R. maximum* and *K. latifolia* in the understory layer contributes to changes in forest structure and composition. Such changes result from decreases in the recruitment of canopy tree seedlings due to light and water competition with understory shrubs (Nilsen *et al.* 2001). Secondary effects of the presence of a dense undergreen layer include reduced seed rain, inhibited mycorrhizal synthesis (Walker *et al*. 1995), and lower bacterial or invertebrate activity related to the deep and slowly decaying litter typical under thickets (Rivers *et al*. 1999). The failure of regeneration by canopy tree seedlings on plots with evergreen shrub thickets has been studied extensively (Minkler 1941, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al*. 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002).

In this study, the spatial extent of the *R. maximum*- and/or *K. latifolia*-dominated evergreen understory layer was assessed using Landsat Enhanced Thematic Mapper (ETM) imagery and ancillary information in two study areas in the central Appalachian highlands. The overall objective of the research was to evaluate the prevalence, temporal dynamics, and consequent ecological impacts and long term influence of these forest understory plant communities in central Appalachian forests. The specific objective of this paper is to determine the spatial extent of the different types of evergreen understory communities – those dominated by *R. maximum* and/or *K. latifolia* – to the greatest possible degree of accuracy using remote sensing data integrated with other available geographic information.

A new approach is needed to determine the spatial extent of forest evergreen understory communities in Appalachian forests. Space-borne remote sensing data has not been employed to map the forest evergreen understory layer in the Appalachian highlands, although interpretation of aerial photographs has been used in the Southern Appalachians toward this end (Dobbs 1995). Automated procedures have not been developed to apply increasingly available, inexpensive, and repeatable multispectral remote sensing data to this challenge. The national land cover data set (NLCD), produced by the multi-resolution land characteristics (MRLC) consortium (Vogelmann *et al*. 2001) used Thematic Mapper (TM) image data to map land cover classes on a regional scale, but only identified three forested classes – deciduous, evergreen, and mixed. The NLCD classification refers to the proportion of canopy tree species that have a deciduous habit, but does not include understory layer shrubs, thereby limiting its usefulness in Appalachian forests. In the NLCD, areas that have a 'winter-green' vegetative cover beneath deciduous trees are mapped as 'mixed' or 'evergreen'.

To demonstrate the limitations of the NLCD in characterizing forested areas containing an evergreen understory, the NLCD classification was evaluated with respect to actual vegetation composition at the locations of a series of plots for which vegetation surveys had been conducted. Plots containing at least 25 percent cover of evergreen understory species, but with a predominately deciduous overstory were compared to the NLCD classification. These plots were most commonly misclassified as mixed canopy forests (Table A8), although it is arguable that none of the NLCD forest classes are technically correct for the vegetation assemblages on these plots. In the Ridge and Valley study area, the comparison of mapped NLCD classes to ground measurements yielded an overall accuracy of 56 percent. In the

Allegheny Plateau study area, the overall accuracy was 47 percent. The classification errors were related to the amount of evergreen understory cover present on these plots, with the evergreen canopy misclassification most often attributed to plots containing the highest cover (see Table A8). The assessment of the NLCD data was undertaken to evaluate the inadequacy of the NLCD classification scheme (Anderson level II) to assess the spatial patterns of the evergreen understory layer species *K. latifolia* and *R. maximum* in Appalachian forests.

3.2 Methods

3.2.1 Study Areas

This research was conducted in two study areas within the central Appalachian highlands (Figure 1.3). These areas were selected for their differing topographic and climatic environments. One study area was located in the warmer and drier Ridge and Valley physiographic province (encompassing the Green Ridge and Buchanan State Forests in Maryland and Pennsylvania), and the other was located in the cooler and wetter Allegheny Plateau (containing the Savage River, Potomac, and Forbes State Forests). Much of the areas within these study areas are public forest or game lands, and consequently experience less intensive development and logging pressure than adjacent privately held land. Because of differences in topography and climate, as well as land use history, the forest community composition and structure of the forest communities in these two study areas were dissimilar. The polygonal regions of both study areas were located in the heart of the geographic range of *K. latifolia* and *R. maximum* (Figures 1.1 and 1.2), and were delineated to avoid human-dominated areas lying outside of publicly-held lands.

3.2.2 Ridge and Valley Province

Green Ridge State Forest (GRSF) and Buchanan State Forest (BSF) lie in the Ridge and Valley physiographic province in western Maryland and south-central Pennsylvania. The largest concentration of evergreen understory vegetation is located in an area of BSF known as the Martin Hill Wild Area, in which the forests were originally harvested in the late 1800s and early 1900s. The area that is now GRSF in Maryland was heavily cut for timber, tanbark, and hoop poles between 1879 and 1910, and wildfires were common in the regenerating forest for a number of years thereafter (Mash 1996). In the early and middle of the 20th century, this area was planted in fruit (primarily apple) orchards (Mash 1996).

The current forest of the Ridge and Valley study area was composed primarily of deciduous trees (oak-dominated) mixed with a lesser amount of coniferous trees in the canopy, and has been defoliated numerous times in the last two decades. Chestnut oak (*Quercus prinus*) comprised 24 percent of the total basal area, followed by red oak (*Quercus rubra*) at 16 percent, white oak (*Quercus alba*) at 13.5 percent, scarlet oak (*Quercus coccinea*) at 7.5 percent, and black oak (*Quercus velutina*) at 6.5 percent (Chastain, unpublished data). Various pines (*Pinus virginiana, strobus, rigida, and pungens*) made up 9 percent of the overall basal area in this study area. These forests are largely 50 to 75 years in age (CFI data, unpublished).

Yearly average minimum and maximum temperatures for this study area were 2.3 and 15.8°C, with temperatures rarely exceeding 32°C in the summer months, but regularly dipping below -10°C in the winter (Stone and Matthews 1974). Elevation ranges from 123 to 845 meters, with steep northeast-southwest trending ridges in the GRSF and a larger contiguous upland area in the Martin Hill section of the BSF. The annual precipitation range was 896 – 1297 mm (averaging 1023 mm) for the period 1983-1998.

3.2.3 Allegheny Plateau

The Allegheny Plateau study area was considered part of the mixed mesophytic forest by Braun (1950). As with the Ridge and Valley, this area was largely cut in the 20th century, but has regenerated naturally in the interim. This study area has been periodically defoliated by the gypsy moth caterpillar since the 1980s. The forest canopy in this study area was primarily deciduous with localized areas dominated by hemlock (*Tsuga canadensis*). Data from 105 field plots indicated that red oak (*Quercus rubra*) made up 25 percent of the total basal area, followed by red maple (*Acer rubrum*) at 18 percent and chestnut oak (*Quercus prinus*) at 17 percent (unpublished data). Hemlock accounted for 5.5 percent of the total basal area. American chestnut was an important component of these forests previous to its extirpation in the early to mid 20th century due to the blight caused by the fungus *Cryphonectria parasitica* (Braun 1950). The elevation range for the Allegheny Plateau was 304-986 meters, with a humid continental climate characterized by severe winters and mild summers. The annual precipitation range between 1983 and 1998 was 913 – 1490 mm, with an average of 1216 mm.

3.3 Landsat Data

Spring leaf-off, snow-free Landsat ETM imagery was employed to discriminate the evergreen understory beneath a deciduous forest canopy. Late March or early April imagery were selected as anniversary date images to facilitate the change detection analyses presented in Chapter 4. Evergreen understory community mapping employed the March 31, 2000 Landsat ETM from path16 rows 32 and 33. The image was geographically referenced to UTM zone 17 NAD 83 coordinates using 52 ground control points (GCPs) that were identifiable on both the image and USGS 1:24,000 scale quadrangle maps. The resulting average root mean square error (RMSE) was .57 for the portion of the image that covered the two study areas, indicating that the spatial error between the map source and image data is expected to be less than or equal to one half of a 30x30 meter TM pixel.

An empirical topographic normalization technique was then applied to the TM data to reduce the influence of differential solar illumination related to topography (Allen 2000). An empirical model relating solar illumination angle (cos(i), computed pixel by pixel from a 30 meter digital elevation model and solar azimuth and elevation values for the Landsat overflight) to differential reflectance of forested pixels was developed band by band such that illumination corrected reflectance (R_i) is calculated as:

$$R_i = R_o - \cos(i) * M - B + R(\text{hat})$$

where M and B are regression parameters, R_o is the original reflectance, and R(hat) is the mean reflectance (Meyer *et al*. 1993). Regression parameters for each study area are reported in Table A9. Finally non-forested areas were masked from further analyses using a separate unsupervised classification.

3.4 Image Classification

3.4.1 Optical Imagery

The 6 multispectral Landsat ETM channels contain substantial redundancy which was reduced via principal components to three bands (PC1, PC2, and PC3) explaining 98.2 percent of the variance in the original Ridge and Valley image and 98.4 percent of the variance in the original Plateau image. The two mid-infrared channels (ETM5 and ETM7) were most closely associated with PC1 in both study areas, and the near infrared channel (ETM4) was most highly correlated with PC2. The tasseled cap transformation was also applied to derive the widely used Brightness (soils), Greenness (vegetation), and Wetness (plant canopy and soils) indices (Crist and Cicone 1984, Crist and Kauth 1986).

Also derived were the normalized difference vegetation index (NDVI), computed from ETM data as (NIR – Red) / (NIR + Red), and soil adjusted vegetation index (SAVI), which is calculated as (NIR – red) / (NIR + red + .5). These indices are commonly used as correlates of leaf area, biomass, percent green cover, productivity, and photosynthetic activity (Tucker 1979, Sellers 1985). SAVI has been found to be more successful than NDVI in filtering out “vegetation equivalent noise” (background soil and standing litter reflectance) in complex plant communities (Huete 1989, Van Leeuwen and Huete 1996). Both of these vegetation indices were included in subsequent classification data ‘stacks’, because one purpose of this work was to determine the combination of raw bands and/or derivatives (Table A10) that best delineated evergreen understory plants.

3.4.2 Ancillary Spatial Data

From pilot analyses, it was expected that some confusion would result from attempting to distinguish forest understory communities dominated by *K. latifolia* from those with *R. maximum*. In addition, as noted from the NLCD classification, there was concern regarding confusion of evergreen understory communities with truly mixed oak-pine forests or even forests with regenerating coniferous understories (e.g. white pine, hemlock). It was hypothesized that topographic data could be used to distinguish among evergreen understory species (Franklin 1998), while synthetic aperture radar (SAR) data would help distinguish physiognomic differences (Dobson *et al*. 1996).

Topography

Topographic indices were derived from the 30-meter National Elevation Database (NED) DEM of the study areas. These indices represent measurements of indirect gradients hypothesized to control species distribution (Austin and Smith 1989, Franklin 1995). Topographic indices have also been used to characterize the spatial distribution of species in predictive mapping (Parker 1982, McNab 1989, 1993, Iverson *et al*. 1997), but have infrequently been used with remote sensing data (Frank 1988, Ohmann and Gregory 2002). From the DEM data, the indirect gradients of slope, aspect, elevation, slope position, and slope curvature were derived (Table A4). These indirect gradients act as measurable surrogates to the direct gradients of exposure, moisture availability, temperature, and growing season length. Specifically, these gradients represent the topographic moisture gradients resulting from slope position, exposure, or curvature, that separate *R. maximum* and *K. latifolia* based on their disparate ecological niches.

SAR Image Data

SAR image data was applied in this research in the hopes that it would improve the discernment of areas where the understory layer is dominated by regenerating *T. canadensis* in the Plateau study area and *P. strobus* in the Ridge and Valley study area. The SAR image data was acquired during leaf-off conditions (limiting the interaction with canopy foliage), and data from two different sensors were used to exploit differences in their send and receive modes. SAR image data obtained from both the ERS-2 and Radarsat sensors are acquired in the C-band wavelength (5.7 and 5.6 cm respectively), making them sensitive to objects on the scale of *R. maximum* and *K. latifolia* leaves (Lillesand and Kiefer 1994, Dobson *et al*. 1996). Radarsat sensor sends and receives with horizontal polarization (HH), making it more sensitive to objects that are oriented horizontally, such as evergreen leaves. The ERS-2 sensor sends and receives microwave signals with vertical polarization (VV), so vertically oriented objects reflect more strongly. This may potentially include the needle bundles of *T. canadensis* and *P. strobus*.

Two Radarsat images – obtained on February 18 (ascending) and March 4 (descending), 2000 – were available to test their utility. These dates correspond well with leaf off periods in the study areas examined. The available ERS SAR image was obtained over the study areas on November, 11 1997. The Radarsat and ERS images were despeckled using a 5X5 Lee filter (Lee *et al*. 1994) and variance texture measures were made on a 3X3 window neighborhood (Haack and Bechdol 2000). In addition to the despeckled and texture SAR image data, the two Radarsat images were combined using PCA, and the first two principal components were used to lessen the influence of topography by combining the different look angles in the ascending and descending modes into the principal components. A 6-layer stack of SAR image data derivatives (Table A10) was assessed for its utility to further detect broadleaf evergreen understory vegetation (*R. maximum* and *K. latifolia*) from coniferous evergreen vegetation (*T. canadensis*) present in the Plateau study areas. Only February 18, 2000 Radarsat data (ascending) was available over the Ridge and Valley, so a 3-layer data stack (raw, despeckled, and texture) was used to test the utility of SAR for discerning understory *P. strobus* in this study area (Table A10).

Field Data

Compositional and structural vegetation data was obtained in the Green Ridge and Savage River State Forests in Maryland and the Buchanan State Forest in

Pennsylvania between 1999 and 2002. The plots were laid out as described by Townsend and Walsh (2001), with two crossing 60 meter transect tapes and five sample points located at the end of the transects and at their intersection. This plot size has been determined to be favorable for remote sensing vegetation studies (Justice and Townshend 1981). Basal area was estimated at each of the sample points using the Bitterlich variable plot method (Grosenbaugh 1952, Lindsey *et al*. 1958), and tree height measures (top and bottom of leaf canopy) were taken for three canopy and subcanopy trees each using a laser rangefinder. Heights (top and bottom of leaf canopy) were also noted for all shrub and sapling species present with greater than 15 percent coverage in the immediate vicinity of the sample points to estimate an average height for the shrub/sapling layer. Cover was estimated for the canopy, subcanopy, shrub/sapling, and herb layers as a whole, as well as on an individual species basis. Due to the difficulty encountered in establishing 60 meter transects in the heavy vegetation present in some of the evergreen understory plots, these plots were limited to one 60 meter transect with three sample points - one at each end and one in the middle. A total of 105 vegetation plots were established in the Savage River State Forest in the Allegheny Plateau physiographic province and 108 plots were placed in the Green Ridge and Buchanan State Forests in the Ridge and Valley province. Plots containing over 25 percent cover of either *K. latifolia* or *R. maximum* were used exclusively to assess classification accuracy. When a mixture of *R. maximum* and *K. latifolia* occurred in a plot, it was designated as an *R. maximum* plot if *K. latifolia* cover was 20 percent or less (and vice versa). If both cover types were higher than 30 percent or were somewhat equal (e.g. 25 percent vs. 25 percent), then the plot was designated as a ‘mixed’ evergreen understory plot. Additional observational data and field notes were used to train the supervised classifications of the imagery, so that all of the plot data could be employed to validate these classifications. In the Ridge and Valley, this included 57 plots with complete vegetation surveys and 28 additional plots in which only canopy and understory coverage were recorded (Table A11). 98 survey plots were used to validate the Allegheny Plateau classifications along with 42 less intensive validation plots (Table A11). All field survey and training sites were located on the imagery using differential GPS.

3.4.3 Analytical Methods

Image classifications employed three methods and three combinations of data sets, resulting in a total of nine classification analyses. Landsat data were evaluated individually, then topographic and SAR data were successively added to determine whether accuracy was improved. Only supervised classification methods were tested to take advantage of the extensive training data sets assembled in the two study areas. Maximum likelihood, minimum distance (both implemented in ERDAS Imagine), and decision tree (using S-Plus) classification methods were compared for each combination of data sets. Supervised classification methods using the maximum likelihood and minimum distance decision rules are widely used, whereas decision trees are becoming more prominent in light of their ability to identify the inputs that produce the best separability in classification problems (Hansen *et al*. 1996). Decision trees have been demonstrated to produce robust results for land cover classification in a number of environments and over a spectrum of scales (Friedl and Brodley 1997, Freidl *et al*. 1999, Hansen *et al*. 2000, Joy *et al*. 2003, de Colstoun *et al*. 2003). Decision tree-based models differ from linear and additive logistic models for classification problems, in that they recursively split the data to form homogeneous subsets. The layered classification approach applied in decision trees represents a simpler method, with classes forming at each step using the fewest possible variables (Lillesand and Kiefer 1994). An example of the recursive design of a classification decision tree can be seen in Figure 3.2. An overall accuracy of 80 percent was selected as a minimum target accuracy rate, and was exceeded in both study areas.

3.5 Results

3.5.1 Separability of Evergreen Understory Communities

Landsat, SAR, and topographic data was selected for input into the supervised classifications by examining statistical separability of 'signatures' created from training data sets. Training data sets for different evergreen vegetation categories were interactively derived by drawing polygons in which to sample through the data 'stack' of Landsat, SAR, and topographic data in known locations of that vegetation community type. Identification of Landsat spectral bands, their derivatives, SAR data, and topographic information that are applicable to discerning different evergreen understory communities through statistical analysis is valuable for future evergreen understory mapping endeavors. In the Plateau study area, Landsat ETM bands 5 and 7 (1.55 - 1.75 µm and 2.09 - 2.35 µm) proved to be most useful in the

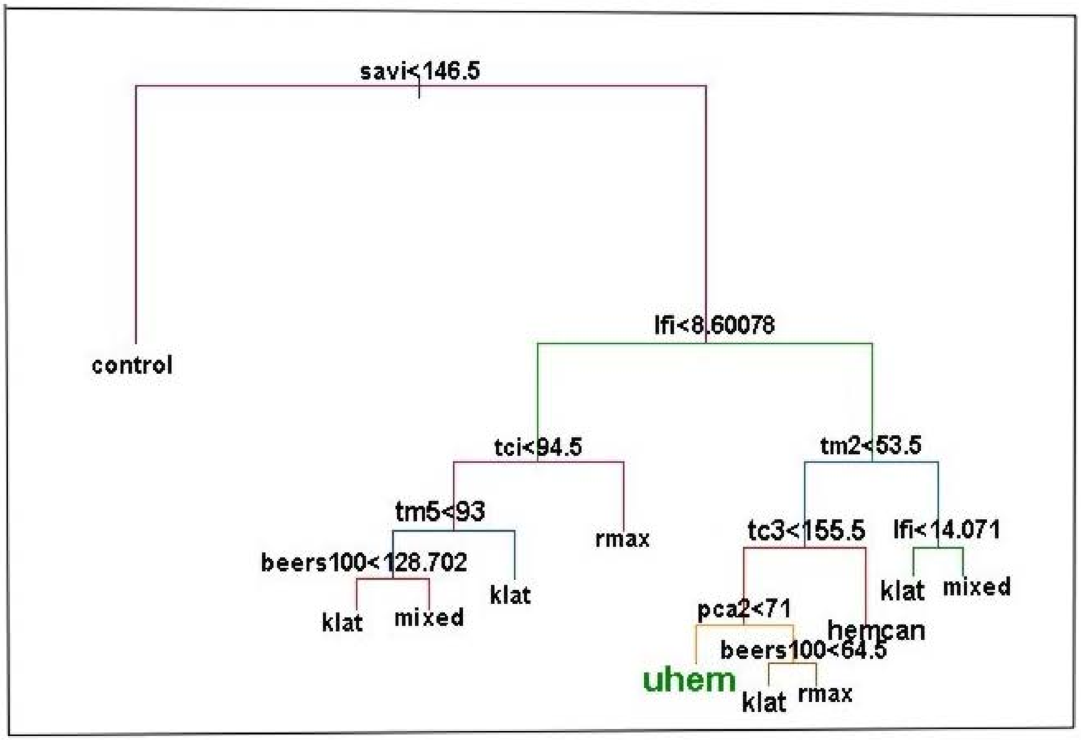


Figure 3.2: Classification tree used to generate an evergreen understory classification scheme for the Allegheny Plateau study area using optical and topographic information. The ‘uhem’ (understory hemlock) class generated from this classification was merged with the results from a maximum likelihood classification to produce a final evergreen understory map for the Allegheny Plateau, which was then used in this research.

separation of *R. maximum* and *K. latifolia* understory communities. PC2 and PC3, Greenness, and SAVI distinguished winter-green vegetation types based on their level of greenness, with training data sets for *K. latifolia*-dominated community and hemlock understory classes having the lowest mean values, and the training data set for the hemlock canopy class the highest mean value (Figure 3.3). ETM5 and ETM7 are sensitive to green vegetation moisture content, and have been shown elsewhere to be sensitive to understory vegetation (Stenback and Congalton 1990). Specifically, *K. latifolia* leaves exhibit greater moisture content than *R. maximum* during the winter/spring because the stomata on *R. maximum* leaves remained closed during winter, and were not photosynthetically active. In contrast, the stomata of *K. latifolia* leaves were open during March 31, 2000, when the maximum temperature (15° C) was high enough for *K. latifolia* stomata to open (Nilsen 1992). The topographic variables with the greatest degree of separability information were the relative slope position (RSP), Beers-transformed slope aspect, and TCI. *R. maximum* was discernable from *K. latifolia*-dominated and mixed understory communities as occurring at relative slope positions with higher wetness (TCI) values. In the decision tree classifications performed, ETM5, LFI, and BEERS were the most frequently used input variables for separating the different winter-green classes, followed by ETM1-4 and NDVI (Table A12).

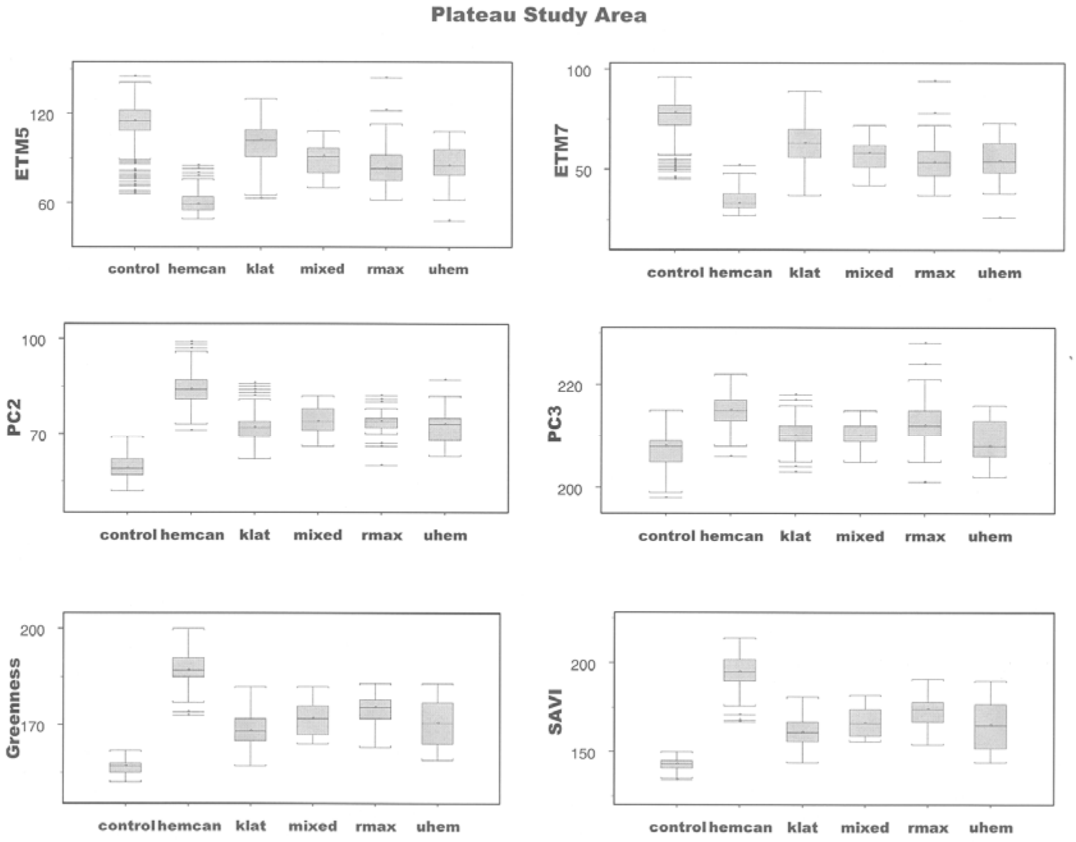


Figure 3.3: Boxplots of spectral data used to train the maximum likelihood and minimum distance classifications in the Allegheny Plateau study area. These plots illustrate the separability between vegetation classes for the different Landsat TM bands and derivations used in these classifications.

SAR data did not exhibit improved separability compared to spectral and topographic data, but were nevertheless evaluated. The broadleaf evergreen vegetation (*K. latifolia* and *R. maximum*) exhibited higher backscatter response to the active sensor compared to understory hemlock, but difference in their means was not statistically significant ($p > .05$). It is therefore uncertain whether reflectance differences were due to the moisture content or leaf orientation of these species, or some other target characteristic.

SAVI and NDVI are very similar and were both effective in separating the study area into winter-green (dark) and brighter (control; no evergreen understory) areas. The primary input variable selected in all of the decision trees for this study area was therefore SAVI or NDVI, regardless of the input classifier data. All classification trees are not presented here because of the large number of analyses, but a tree diagram for the Plateau study area shown in Figure 3.2 serves as an example. Landsat ETM2 and ETM5 were employed in the classification, as were Wetness and PC2 (correlated with the NIR channel). Topographic variables LFI (topographic exposure), TCI (topographic moisture or wetness), and Beers were employed when topographic variables were included. LFI bifurcated the upslope *K. latifolia*, *R. maximum*, and mixed understory areas from the lower slope portions of those communities. In upslope locations, TCI separated the moisture-loving *R. maximum* communities from *K. latifolia*, which tolerates drier conditions. On lower slopes, ETM2 (sensitive to green reflectance) separated the denser and hence greener hemlock and *R. maximum* communities from the mixed and *K. latifolia* communities, which generally are sparser in coverage. In all of the Plateau decision tree classifications created, ETM5, LFI, and BEERS were the most often used input variables (Table A4). The decision tree models were coded into a GIS and mapped for later comparison (see Figure 3.7)

In the various classifications performed for the Ridge and Valley study area, the spectral variables that proved valuable for the separability of the different winter-green classes were ETM4, ETM5, ETM7, PC1, Brightness, Wetness, and SAVI. As in the Plateau study area, the topographic variables that were of use were the RSP, LFI, and TCI, although the topographic training data was not as useful in separating the vegetation classes as was the optical data (Figure 3.4 and 3.5). Especially useful separating out the different classes in the maximum likelihood classification using optical data alone was ETM5, ETM7, PC1, Wetness, Brightness, and SAVI (Figure 3.4), while ETM4, PC2, Brightness, and Greenness most often were used in the decision tree classifications performed (Table A12). SAR data again did not exhibit improved separability compared to spectral and topographic data, but available Radarsat data were evaluated nonetheless to test the resulting influence on accuracy.

3.5.2 Map Accuracy

Maps derived from the classifications exhibited patterns of species distribution that were similar to each other, but also had notable differences (Figures 3.6 and 3.7). Maps made using SAR data were noisy, displaying the ‘salt and pepper’ patterns

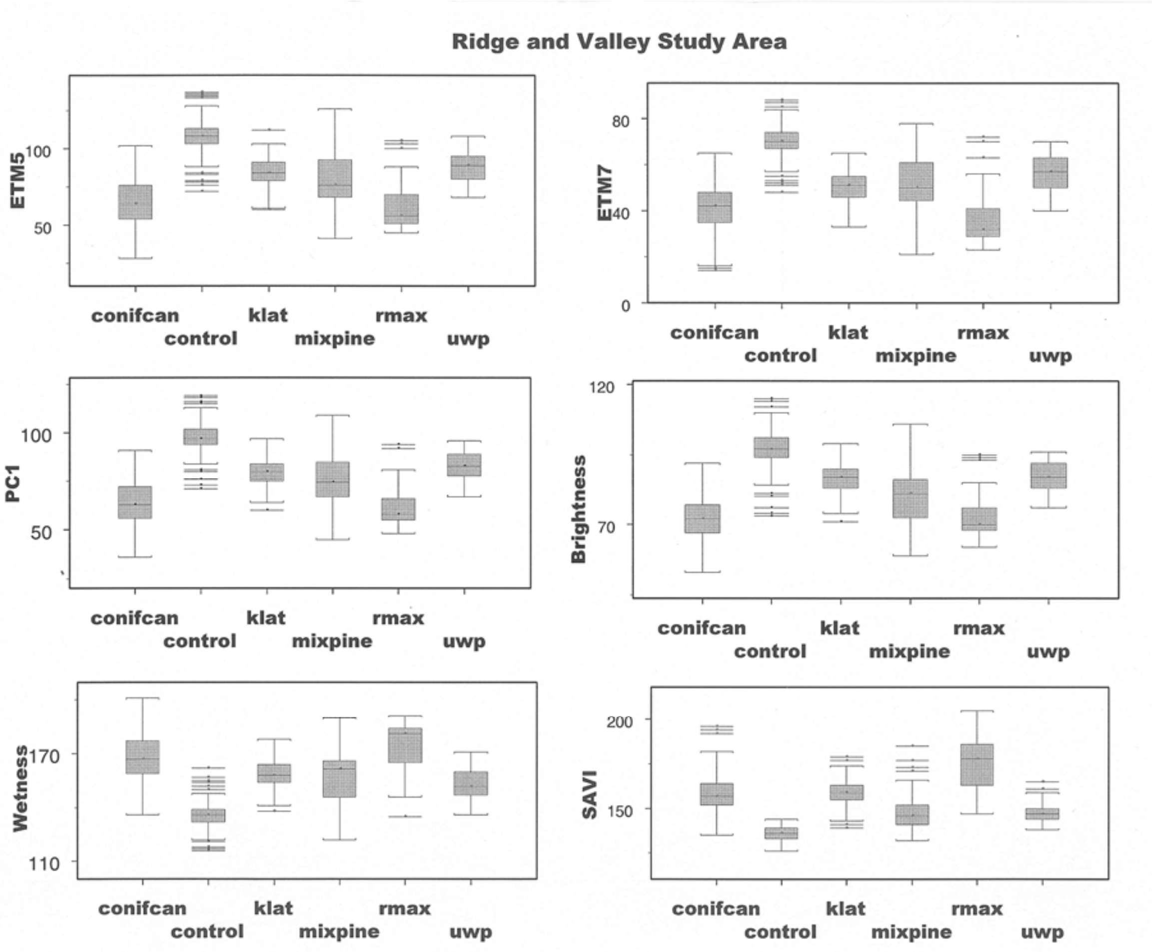


Figure 3.4: Boxplots of spectral data used to train the maximum likelihood and minimum distance classification in the Ridge and Valley study area. These plots illustrate the separability between classes for the different Landsat ETM bands and derivations used in these classifications.

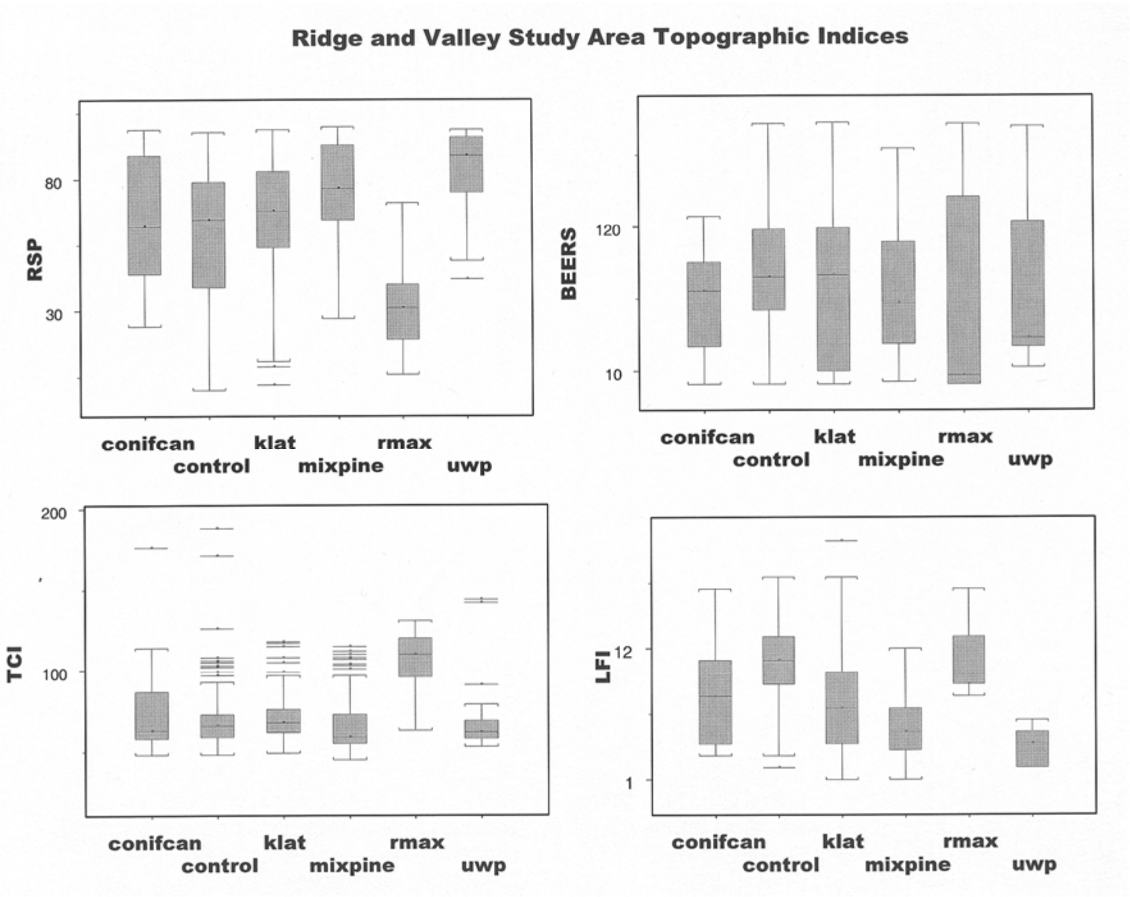


Figure 3.5: Boxplots of topographic data used to train the maximum likelihood and minimum distance classification in the Ridge and Valley study area. These plots illustrate the separability between classes for the various topographic indices used in these classifications.

frequently associated with SAR maps. Despite the principal component transformation of the Radarsat data in the Plateau study area, strong topographic bias was apparent on the resulting maps. Using the 140 validation locations on the Allegheny Plateau and 85 on the Ridge and Valley study area (Table A11), overall accuracy, user's accuracy (omission error), producer's accuracy (commission error), as well as the Kappa statistic (the improvement of the classification over chance agreement; Congalton 1991, Congalton and Meade 1983) were examined (Table A13).

In the Ridge and Valley study area, the best classification was the maximum likelihood supervised classification using spectral data alone (Table A13). Although the maximum likelihood classification using spectral and topographic information had similar overall accuracies and K_{hat} measures, visual inspection of areas outside the validation data revealed that the addition of topographic data led to the over-estimation of *R. maximum* and *K. latifolia* in the GRSF portion of the study area. The misclassified areas were actually winter-green due to the presence of conifers in former agricultural areas. Areas marked by extensive agricultural land use history are typically free of *K. latifolia*, with areas with a lesser extent of agricultural history acting as refugia for this species (Wilson and O'Keefe 1983). In such cases, land-use history superceded the predictive value of topography in land-cover classification. The overall accuracy of the maximum likelihood classification of the optical data alone was 82.3 percent (Table A14a). One source of misclassification error

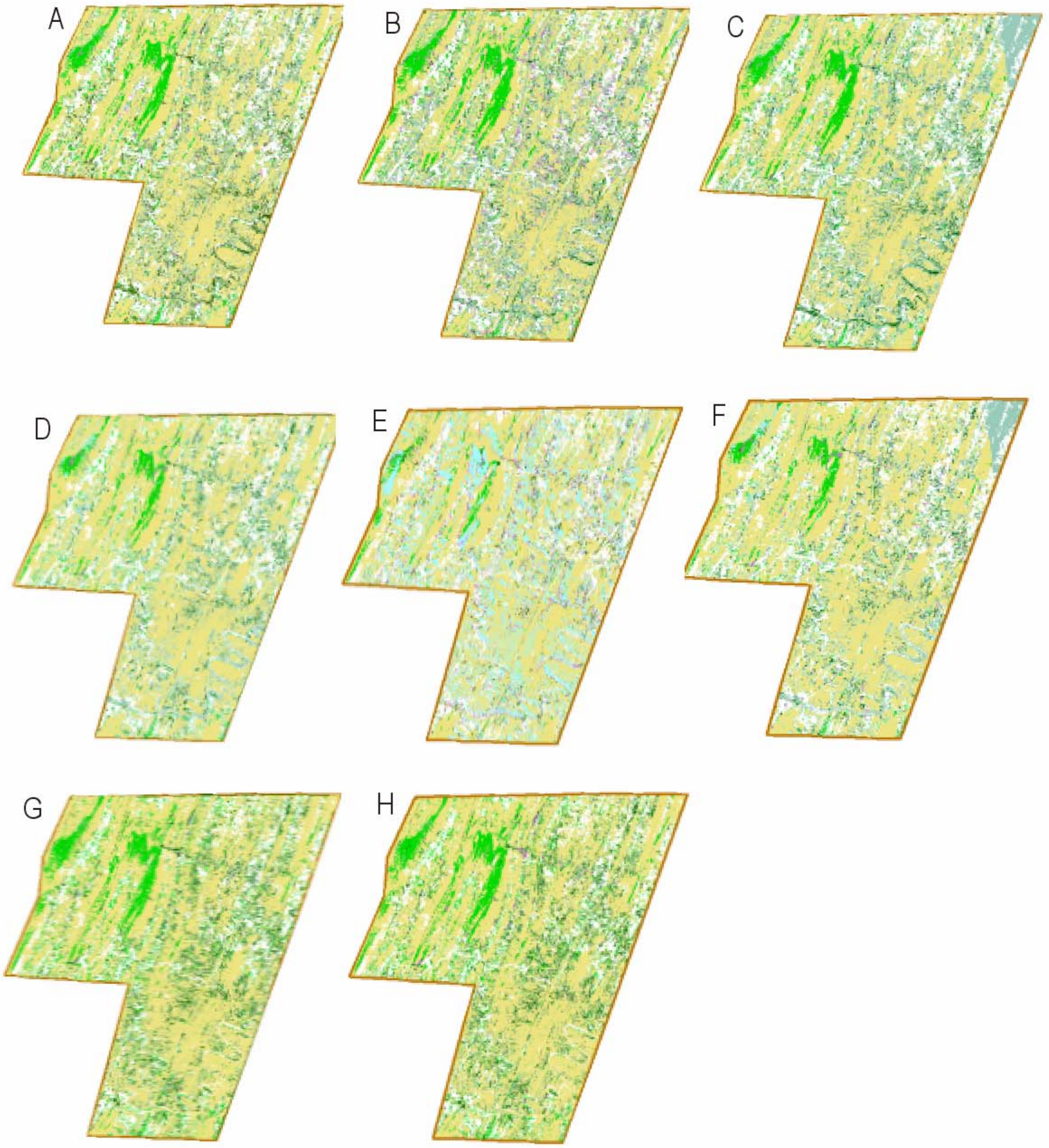


Figure 3.6: Classification results for the Ridge and Valley study area obtained from A) maximum likelihood using optical data only, B) maximum likelihood using optical and topographic data, C) maximum likelihood using optical, topographic, and SAR data, D) minimum distance using optical data only, E) minimum distance using optical and topographic data, F) minimum distance using optical, topographic, and SAR data, G) decision tree using optical data only, and H) decision tree using optical and topographic data. See Figure 3.8 for map key.

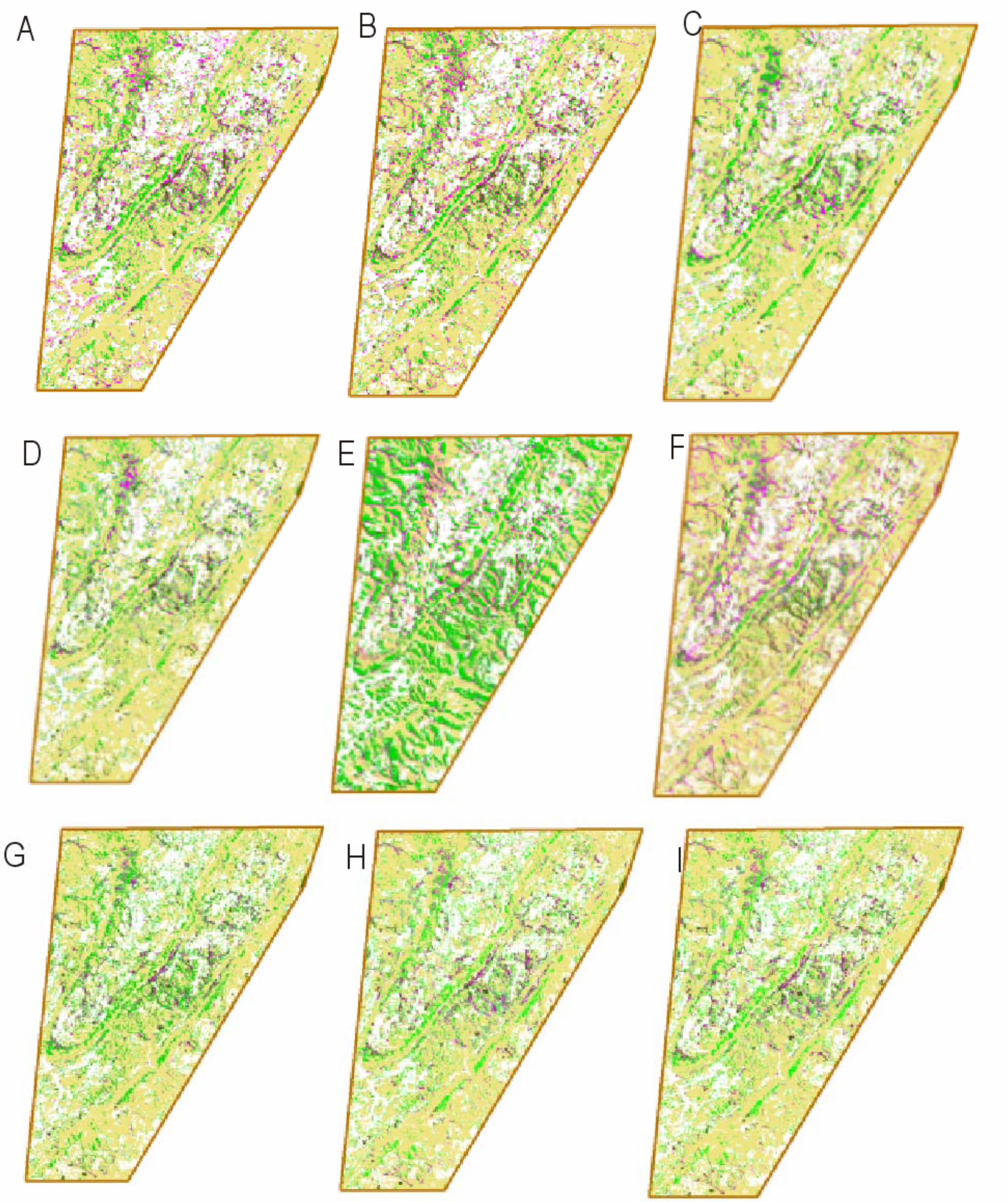


Figure 3.7: Classification results for the Allegheny Plateau study area obtained from A) maximum likelihood using optical data only, B) maximum likelihood using optical and topographic data, C) maximum likelihood using optical, topographic, and SAR data, D) minimum distance using optical data only, E) minimum distance using optical and topographic data, F) minimum distance using optical, topographic, and SAR data, G) decision tree using optical data only, H) decision tree using optical and topographic data, and I) decision tree using optical, topographic, and SAR data. See Figure 3.9 for map key.

(occurring three times) involved confusion of areas with less than 30 percent of *K. latifolia* cover with no evergreen understory present. Because the primary goal of this classification entailed discernment of evergreen understory shrub communities from other winter-green vegetation (conifers) and forested areas that do not contain this vegetation, the conifer classes were combined to examine the resulting classification accuracy. After combining the conifer classes, the overall accuracy of this classification was 87.1 percent (Table A14b).

In the Allegheny Plateau study area, the maximum likelihood supervised classification using spectral and topographic data provided the highest accuracy (80 percent), but did not include an understory hemlock class due to insufficient training data for the maximum likelihood decision rules. Understory hemlock was more accurately delineated by the rules specified in the recursive decision tree classification (50 percent producer's accuracy), so the final map employed the hemlock portion of the classification tree data (Figure 3.2). This hybrid approach utilizes the best aspects of the two methodologies to produce a superior overall map (82.9% overall accuracy, Table A15) compared to individual classifications (Townsend and Walsh 2001). As in the Ridge and Valley study area, one of the sources of misclassification error (occurring twice) involved confusion of areas with low *K. latifolia* cover (30 percent) as being free of evergreen understory.

The final accuracy assessment of the Allegheny plateau classification exceeded the pre-set goal of 80 percent (82.9 percent) with producer's and user's accuracies high in most of the categories (Table A15). The low user's accuracy result for *R. maximum* (50 percent) is due largely to confusion with *K. latifolia* communities, but in half of those instances a small amount of *R. maximum* was also in the understory at the validation point. In fact, half of the overall cases of confusion in the Allegheny Plateau classification occurred among the *R. maximum*, *K. latifolia*, and 'Mixed' broadleaf evergreen vegetation classes (see Table A15), so the discernability of these vegetation communities from 'control' and hemlock-containing classes is excellent.

The evergreen understory community maps derived for the Ridge and Valley and Allegheny Plateau study areas (Figures 3.8 and 3.9) illustrate distinct topographic patterns in both study areas. In the optical data classification of the Ridge and Valley study area, *K. latifolia*- or *R. maximum*-dominated evergreen understory vegetation communities cover over 6 percent of the total forested region. Most of this coverage is *K. latifolia*-dominated communities (5.9 percent of total forested area), with *R. maximum*-dominated communities covering only 245 hectares (0.25 percent). In the merged maximum likelihood-decision tree classification of the Allegheny Plateau study area, *K. latifolia*- and/or *R. maximum*-dominated communities cover 26.6 percent of the total forested area. The total area of *K. latifolia*-dominated evergreen understory communities is more than the total of the *R. maximum*-dominated and mixed evergreen areal extent combined (see Table A16). The concentration of evergreen understory increases towards the western portion of the study area. Apparently forests underlain by thick evergreen understory vegetation have historically characterized this region, as the early explorer Cristofer Gist reported

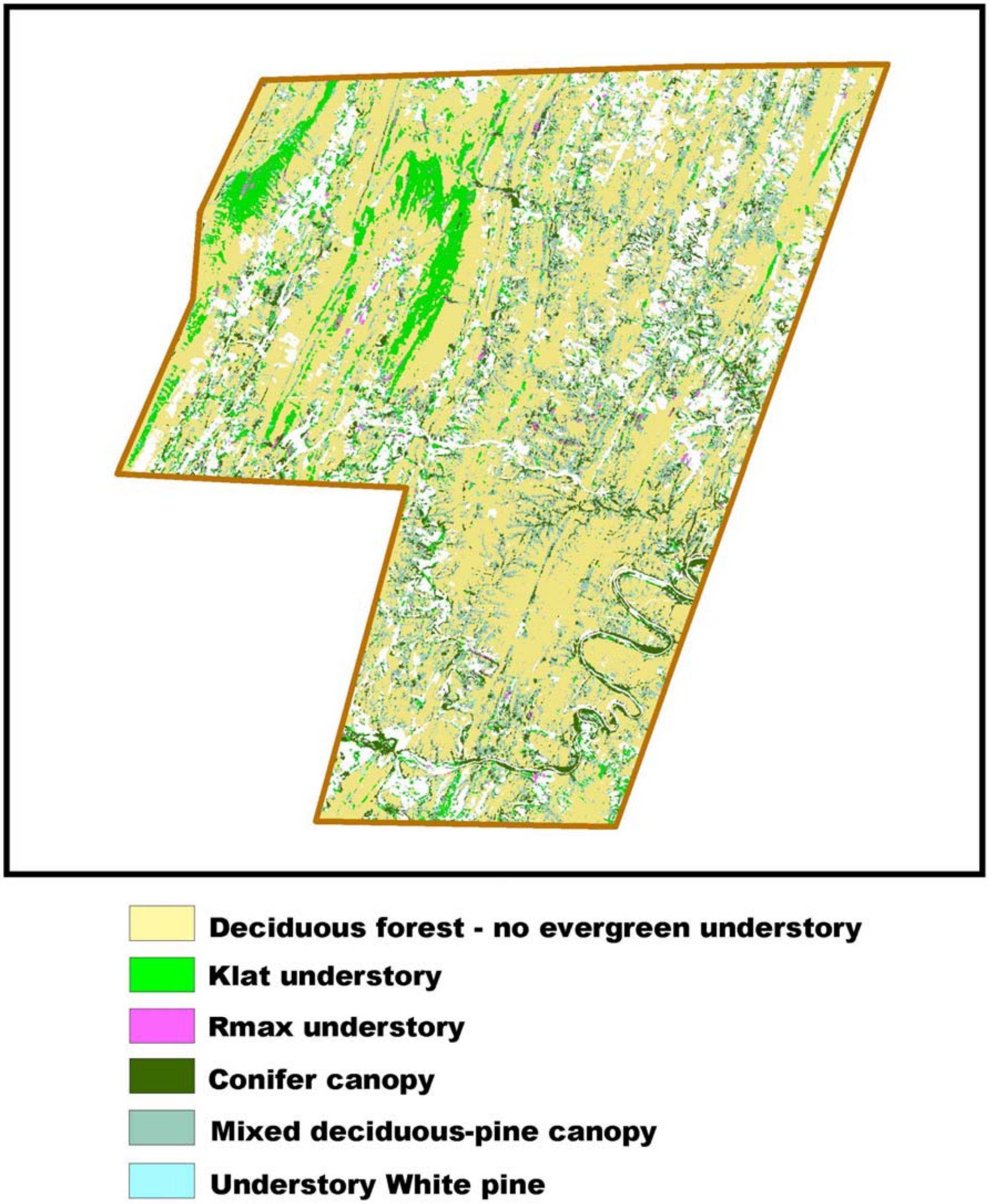


Figure 3.8: Maximum likelihood classification results using optical data only for the Ridge and Valley study area.

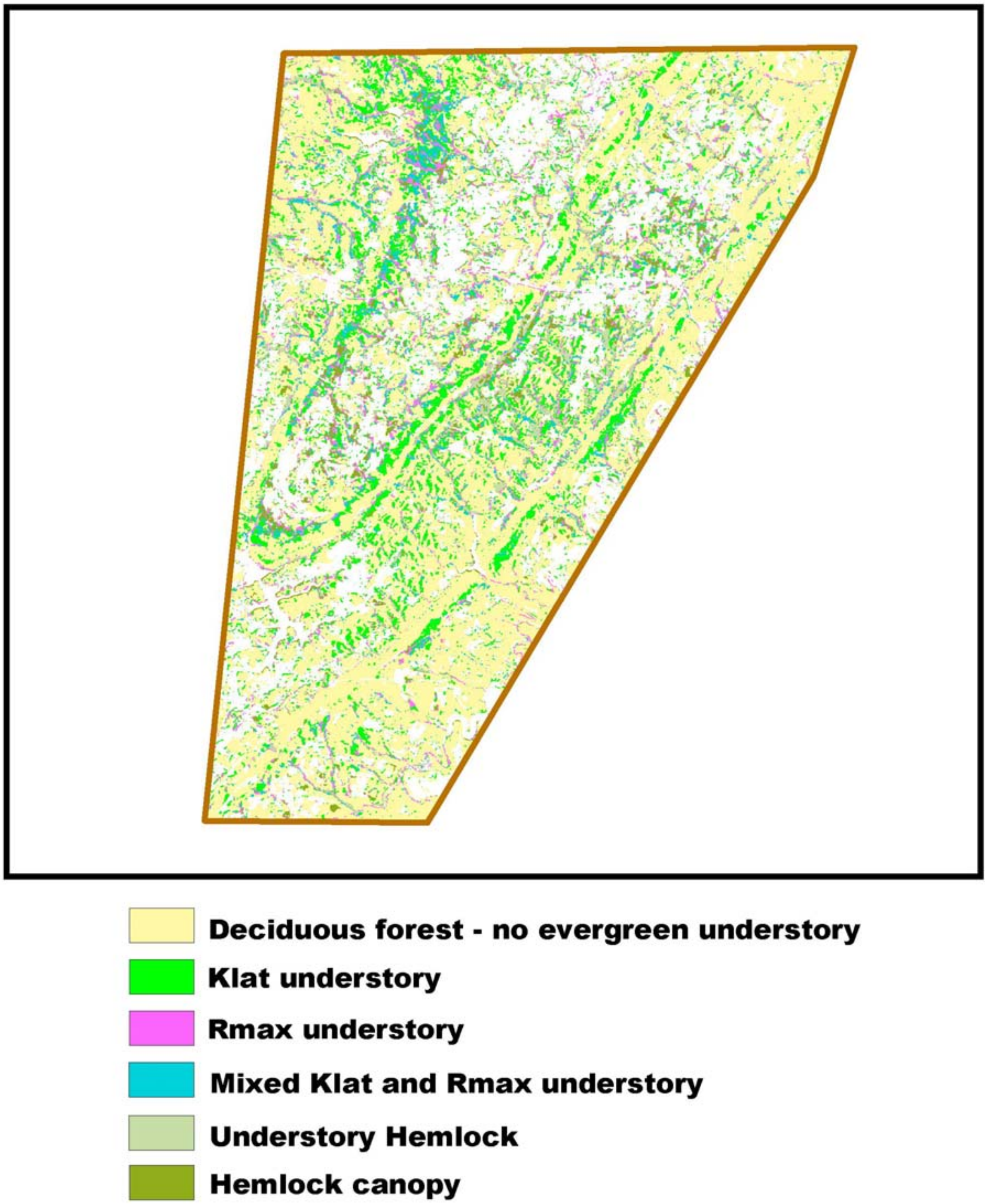


Figure 3.9: Merged maximum likelihood and decision tree classification results for the Allegheny Plateau study area using optical and topographic data.

spending two days cutting through an immense laurel thicket on an exploratory trip through the area in the eighteenth century (Robison 1960). This area has since become known as the 'Laurel Highlands'**.**

3.6 Discussion and Conclusions

A highly accurate classification of the evergreen understory was obtainable using Landsat images and topographic data. Although hyperspectral and radar image data did not enhance map accuracy of these communities on the landscape scale, the cost benefit ratio associated with using Landsat TM data should be considered high, especially considering the potential ecological importance and prevalence of these communities in some areas (i.e. Allegheny Plateau) and the low cost and wide availability of Landsat TM and USGS digital elevation data. A number of the spectral bands (ETM4 and ETM5) and derivatives (PC2, Brightness, and Greenness) of Landsat TM image data proved useful in discerning evergreen understory communities and parsing out those dominated by *R. maximum* and/or *K. latifolia* from other winter-green vegetation. In addition, topographic information proved useful in improving classification accuracy in areas not impacted by an intensive land use history. For example, it became apparent from this research that land use history was a confounding factor to the distribution of evergreen understory communities in the Ridge and Valley province. Whereas much of the literature pertaining to the distributions of *R. maximum* and *K. latifolia* in Appalachian forests focuses on topo-edaphic constraints (Davidson 1966, Romancier, 1970, Monk *et al.* 1985, Lipscomb and Nilsen 1990a, 1990b, Muller 1991, but see Wilson and O'Keefe 1983), these results indicate that the influence of land use history as a regional-scale constraint to their distributions must also be recognized.

Knowledge of the spatial patterns of evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* on the landscape and regional scales is valuable to gain an understanding of their impacts on forest structure and functioning. These impacts include the potential inhibition of canopy tree regeneration, forage and refuge for wildlife, and water quality maintenance. The maps of evergreen understory community types produced in this research represent a significant step towards a better understanding of the landscape level role of the evergreen understory, because information on their spatial extent and patterns is not otherwise available from existing data sources. For example, CFI and forest inventory and analysis (FIA) plot survey data do not contain information on shrub layer vegetation and the classified forest types in the NLCD maps do not contain a category for deciduous forests underlain with broadleaf evergreen understory communities.

Limitations associated with synoptic remote sensing of forest vegetation communities tend to decrease the classification accuracy of forest evergreen understory plant communities – even when a deciduous forest predominates and high quality leaf-off imagery is available. This is intrinsic to the composition of the vegetation communities themselves, and has confounded previous efforts to map understory vegetation in forests (Stenbeck and Congalton 1990). First, *R. maximum* often occurs in riparian areas, where it may co-exist with or lie underneath conifer (primarily hemlock) cover (Oosting and Billings 1939), thus leading to confusion and misclassification between hemlock and *R. maximum* communities. In addition, the effect of bright components of the forest such as leaf litter and the wood from the leaf-off deciduous trees (standing litter) causes the spectral response of evergreen understory vegetation to vary in an unpredictable manner compared to the response from a pure green canopy (Van Leeuwen and Huete 1996). Pixels with evergreen understory cover therefore contain a mixed signal, and if the evergreen understory cover is light, the background forest floor litter layer can saturate the signal from the evergreen target. Because of these factors, it is expected that *R. maximum* and *K. latifolia* will be under-estimated to some degree even in the best of classifications using remote sensing data.

In this study, errors may have been introduced from numerous sources regardless of standards of image processing. Even slight misregistration or GPS mislocation can result in interpretation errors. In addition, the threshold to identify an evergreen understory (30 percent cover for *K. latifolia*) potentially led to confusion, as plots with significant *K. latifolia* coverage (25 or 28 percent, for example) were treated as control plots (no evergreen). Nevertheless, these analyses suggest that the coverage of an evergreen understory needs to exceed 30 percent before reliable identification can occur using remote sensing data.

The inclusion of ancillary variables proved to be marginally useful in the classification of evergreen understory communities. Topographic variables were valuable for the accurate classification of these understory communities in regions where land use history was not intense, but led to confusion with conifer species in the southern (GRSF) portion of the Ridge and Valley study area, an area with a considerable human history (Mash 1996). The use of SAR image data from the Radarsat and ERS-1 sensors to detect and classify evergreen understory community types in the two study areas did not improve results, most likely due to bias created from differential response caused by topographic relief. Also, despite being leaf-off, the presence of tree trunks, limbs and branches probably interfered with SAR responses to evergreen understory types.

Hyperspectral image data may have improved the classification accuracy of evergreen understory communities in this study, but because most available imagery was at least partially leaf-on, this data source was not tested. Previous research has shown that the accurate detection of understory vegetation components using hyperspectral imagery becomes difficult once crown closure exceeds 25 percent (Wilson and Ference 2001). Because of its sensitivity to vegetation status, moisture and biochemical content, leaf-off hyperspectral data would likely have proved valuable in accurately discerning different winter-green vegetation, especially in revealing variations in evergreen understory communities where *K. latifolia* and *R. maximum* are mixed in varying proportions. The price for hyperspectral image data (i.e. EO-1 Hyperion, which follows one minute behind the orbit of the Landsat 7 platform) will continue to decrease and its availability increase over time, and its utility will undoubtedly be proven for evergreen understory mapping in Appalachian forests in the near future.

The evergreen understory maps produced in this study have been applied to a number of further research goals: (1) to analyze the changes that have been occurring in these evergreen understory communities over the period of Thematic Mapper data availability (1983 - present) and relate these changes to disturbances resulting from periodic gypsy moth infestation and climatic fluctuations, and (2) to estimate the overall biomass of the *K. latifolia* and *R. maximum* in these study areas. These estimates have been obtained by regressing tasseled cap greenness with plot-measured stem densities scaled up to the spatial extent of the areas identified in this research as being dominated by *R. maximum* and/or *K. latifolia*. From these estimates, their total carbon sequestration potential and influence on nitrogen cycling have been modeled on the landscape scale.

The maps and spatial extent measures produced in this research have also pointed out differences between the two physiographic provinces studied with regard to the potential for landscape scale persistence of evergreen understory communities dominated by *K. latifolia* and *R. maximum*. Evergreen understory communities covered 26.7 percent of the forested area in the Allegheny Plateau study area, with 43 percent of that area containing *R. maximum*. In contrast, land use history and geological constraints have limited the coverage of evergreen understory communities to 6.1 percent of the forested area in the Ridge and Valley study area, 96 percent of which is dominated by *K. latifolia*. Communities dominated by *R. maximum* are restricted to small areas located in tight drainages in this province. A potential application of this mapping approach would be to see if similar patterns in the coverage of these understory communities occur in other locations in the Appalachian highlands. Existing range maps for *K. latifolia* and *R. maximum* (Figures 1.1 and 1.2) indicate the potential for continuous coverage over the range of the Appalachian highlands, but perhaps their actual current ranges are characterized by regional gaps coinciding with regional specificities in terms of landscape scale patterns of geology and land use history.

Chapter 4: Impacts of Gypsy Moth Infestation and Drought on Evergreen Understory Communities in the Forests of the Central Appalachian Highlands

Abstract

Growth vigor of forest evergreen understory communities dominated by rosebay rhododendron (*Rhododendron maximum* L.) and/or mountain laurel (*Kalmia latifolia* L.) was tracked in two physiographic provinces of the central Appalachian highlands using remote sensing and dendrochronology. At the landscape scale, analyses of Landsat-derived greenness indicated that the timing of changes in growth vigor was linked temporally to climatic fluctuations and gypsy moth defoliations. Evergreen understory communities dominated by both *R. maximum* and *K. latifolia* increased in greenness in response to gypsy moth defoliation of canopy trees in the Ridge and Valley province (where defoliation was pronounced), whereas only *R. maximum* increased on the Allegheny Plateau. Topographically mediated drought stress was the dominant predictor of greenness in evergreen understory communities dominated by *K. latifolia* in the Allegheny Plateau. Dendrochronological analyses revealed a high amount of variability in the growth vigor of *K. latifolia* and *R. maximum* individuals. However, *K. latifolia* exhibited identical average stem diameter growth rate (1.09 mm yr^{-1}) in both the warmer and drier Ridge and Valley and the cooler and wetter Allegheny Plateau provinces, indicating its high level of drought tolerance. In contrast, the aggregate growth pattern for the moisture-loving *R. maximum* exhibited a faster growth rate in the Allegheny Plateau (1.17 mm yr^{-1}) compared to the Ridge and Valley (0.87 mm yr^{-1}). Growth curve trends and peaks/suppressions among *K. latifolia* and *R. maximum* individuals revealed only marginal temporal association with the timing of climatic fluctuations; however, both releases and suppressions in growth were associated with the timing of canopy tree defoliation by gypsy moth for *K. latifolia* in both provinces and for *R. maximum* in the Allegheny Plateau. Remote sensing analyses did not indicate any spatial spread in the distribution of *K. latifolia* and *R. maximum* between 1984 and 2001.

4.1 Introduction

Forest ecosystems provide a number of societal services and act as an essential template for the welfare of numerous fauna, acting as the source of primary productivity and habitat (Schlesinger 1977, Sedjo 1992, Daily *et al*. 1997, Perry 1998, Aber *et al*. 2000, Currie *et al*. 2003). An important, yet understudied component of the forests of the Appalachian highland region in eastern North America is the evergreen understory layer, which is dominated by the shrubs mountain laurel (*Kalmia latifolia* L.) and/or rosebay rhododendron (*Rhododendron maximum* L.). Dense understories dominated by these species may hinder canopy tree regeneration (Minkler 1941, Wahlenburg and Doolittle 1950, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al*. 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002), slow mineral cycling in forests (McGinty 1972, Thomas and Grigal 1976, Monk *et al.* 1985), or strongly influence the potential for carbon sequestration (McGinty 1972, Thomas and Grigal 1976, Monk *et al*. 1985) and maintenance of water quality (Yeakley *et al*. 1994). In addition, evergreen understory communities contribute to the beauty of Appalachian forests and provide forage and refuge for wildlife (Romancier 1970, Gates and Harman 1980, Thackston *et al*. 1982, Hollenhorst *et al*. 1993, Johnson *et al*. 1995, Spear 1998, USDA 2002). As such, insight into the both the state and dynamics of the growth vigor of *K. latifolia* and *R. maximum* is a fundamental component of a comprehensive understanding of the overall health of Appalachian highland forests and their capacity to provide societal and life-giving services.

Changes in the composition and structure of forest ecosystems are often studied to monitor the health of these ecosystems, to assess their capacity to provide societal services such as water quality maintenance, and to predict their future sustainability. These temporal dynamics are the product of individual responses of a forest's component species to fluctuations in environmental factors as well as the consequent changes in their competitive and other interactions. Macroclimatic fluctuations and periodic disturbances are two primary sources of variations in environmental conditions over time in the central Appalachian highlands forests. Specifically, recurrent drought (Orwig and Abrams 1997, Fekedulegn *et al.* 2003) and gypsy moth (*Lymantria dispar* L.) infestation (Musika and Liebhold 1999) produce instability in the environmental conditions to which the growth of forest plant species respond. As Watt (1947) pointed out, there may in many instances be very little correspondence between the observed structure of a forest community and the current environmental conditions due to the presence of long-lived dominants in the canopy. However, it may be feasible to track temporal variations in environmental conditions affecting the growth of the understory species at much shorter time scales than can be observed in the response of overstory trees. In the central Appalachians, macroclimatic fluctuations (i.e. drought) and periodic gypsy moth infestations may interact to affect a forest community represented as a vertically structured entity, in which the evergreen understory is a critical controlling factor (Figure 4.1). The potential impacts of these exogenous disturbance regimes on the evergreen understory layer are hypothesized to strongly impact both canopy and understory dynamics, with the understory dynamics possibly more easily identifiable from proximal environmental indicators.

In contrast to periodic drought, which affects the growth vigor of canopy and understory species, gypsy moth caterpillars primarily pursue the oak component the forest canopy for sustenance. Evergreen understory species are impacted indirectly in divergent ways after a gypsy moth outbreak. The increase in the amount of light under a defoliated oak canopy enhances the growth of *K. latifolia*, increasing stem growth compared to that

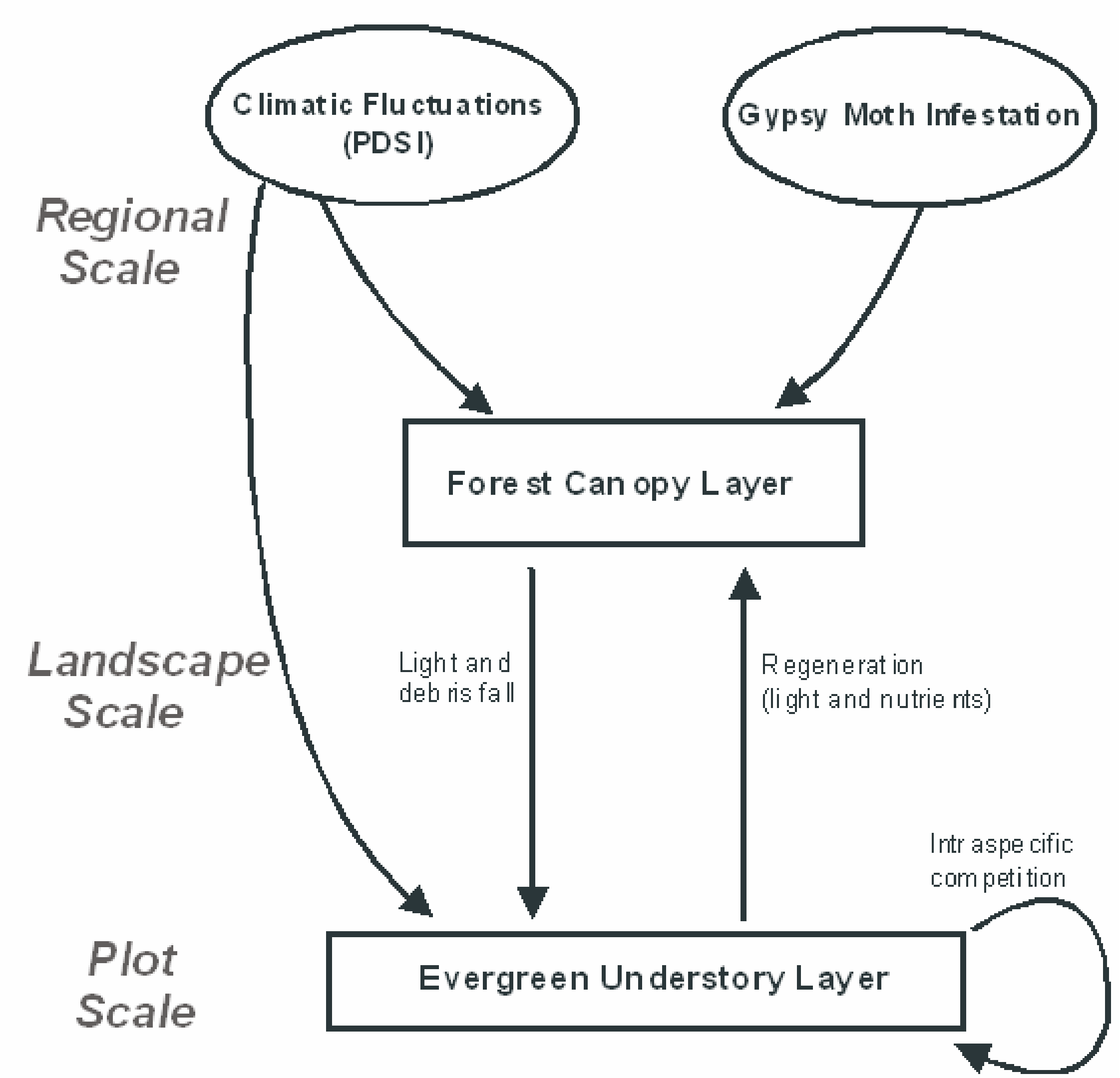


Figure 4.1. Interactions of scales and mechanisms that influence the spatial and temporal patterns of the growth vigor of the *K. latifolia*- and *R. maximum*-dominated evergreen understory communities.

observed under low light conditions (Davidson 1966). Alternately, this increase in light may impair the growth of *R. maximum* individuals, which are very sensitive to their radiance and temperature environment. Specifically, *R. maximum* leaves are adapted in both size and light saturation points to the specific conditions present in their subcanopy microenvironments resulting from the combination of topo-edaphic conditions and the deciduous canopy structure (Whittaker and Garfine 1962, Nilsen 1986, Nilsen *et al*. 1987, Nilsen *et al*. 1988, Lipscomb and Nilsen 1990a, 1990b). On the other hand, the amount of soil moisture has been reported to increase after gypsy moth defoliation has occurred (Stephens *et al*. 1972), thus benefiting both *R. maximum* and *K. latifolia* individuals already present in the understory. Finally, the nitrogen released in the form of frass during the gypsy moth defoliation event is redistributed and made available to evergreen understory layer plants (Lovett *et al*. 2002). *K. latifolia* present in the understory of a defoliated forest stand would theoretically come out with a triple bonus of added light, water, and nitrogen. Impacts on *R. maximum* growth conditions may be much more variable. Would the balance between the increase in water and nitrogen availability and the changes in the radiance and temperature environment be beneficial or disruptive to *R. maximum* growth? Would it be site- and/or event specific?

Various approaches have proven useful in tracking changes in the growth vigor of woody species in forest environments. Direct measurements involving the use of dendrochronology archive the response of trees to macroclimatic environment and the stresses of periodic disturbances such as drought stress, fire, and insect outbreaks (Graybill *et al*. 1982, Schweingruber 1989, Cook et al. 1990a). Indirect methods employing remote sensing imagery can document the landscape scale responses of forest ecosystems over time to changes in their environment (Lambin and Strahler 1994, Coppin and Bauer 1996, Allen and Kupfer 2000, 2001). Direct (ground-based) and indirect (remote sensing) observations are therefore complementary techniques for tracking changes in the condition of forested environments and allow the identification of processes.

This study employs a unique approach to track changes in evergreen understory communities in the central Appalachian highlands. Inexpensive and repeatable remote sensing imagery are combined with the higher spatial and temporal resolution provided by dendrochronology to monitor both landscape level changes in growth vigor (remote sensing) as well as the responses of *K. latifolia* and *R. maximum* individuals (dendrochronology) that form the basis for landscape-level changes. It is commonly stated that scale is a central problem in ecology, and that events and forces that occur at different scales interact in a hierarchical manner (Urban *et al*. 1987, Levin 1992). Thus, the combined behavior of many individuals and/or small-scale events emerges to form observable patterns that are in turn constrained by slower broad-scale phenomena. An observable pattern can be best assessed by applying both bottom-up and top-down approaches to identify relevant mechanisms occurring at different scales. In the context of this study, small-scaled phenomena such as the growth vigor of *R. maximum* or *K. latifolia* individuals combine to influence observable medium scale patterns of forest structure and composition, but all of these variables are simultaneously constrained by regional phenomena such as climate, geology, topography, and periodic insect infestations. Patterns of medium-scaled phenomena such as tree fall gaps in turn influence (constrain and/or promote) the growth vigor of *K. latifolia* and *R. maximum* in a disturbance-prone environment. In this study, two regional scale exogenous factors that are hypothesized to influence the growth of *K. latifolia* and *R. maximum* are investigated: Gypsy moth infestation and drought. Although other local factors also affect these species, gypsy moth infestations and periodic droughts are examined because they are observable and quantifiable at the landscape scale (i.e. spatially), and produce well-documented responses in general forest vigor. Drought periodicity is quantified on a regional (county) scale using the Palmer drought severity index (PDSI, Palmer 1965). The response of *K. latifolia* and *R. maximum* to drought conditions is tested using Parker's (1982) terrain relative moisture index (TRMI), which is an additive combination of landform characteristics derived from elevation data (slope angle, slope position, slope curvature, and slope aspect) developed for use in mountainous terrain to characterize the relative dryness or wetness of specific plot locations. TRMI has been shown to effectively indicate relative moisture conditions within regions (Pinder *et al.* 1997). Previous studies have examined the relationship between drought effects on trees and their topographic position (Orwig and Abrams 1997, Abrams *et al*. 1998, Fekedulegn *et al*. 2003), but using only a qualitative scale of relative moisture availability.

It is hypothesized that regional scale factors (drought and insects) affect forest canopy dynamics at the landscape scale, which in turn impact understory dynamics, with feedbacks occurring between the understory and canopy (Figure 4.1). In this study, remote sensing data and information about drought and gypsy moth defoliation will be used to quantify regional scale impacts whereas dendrochronology will be used to assess plot scale dynamics of the growth vigor of evergreen understory species *K. latifolia* and *R. maximum*. These analyses will be linked to demonstrate the landscape scale interactions between different forest strata and the manner in which disturbance responses of individual shrubs collectively define the growth vigor of evergreen understory communities.

4.2 Study Areas

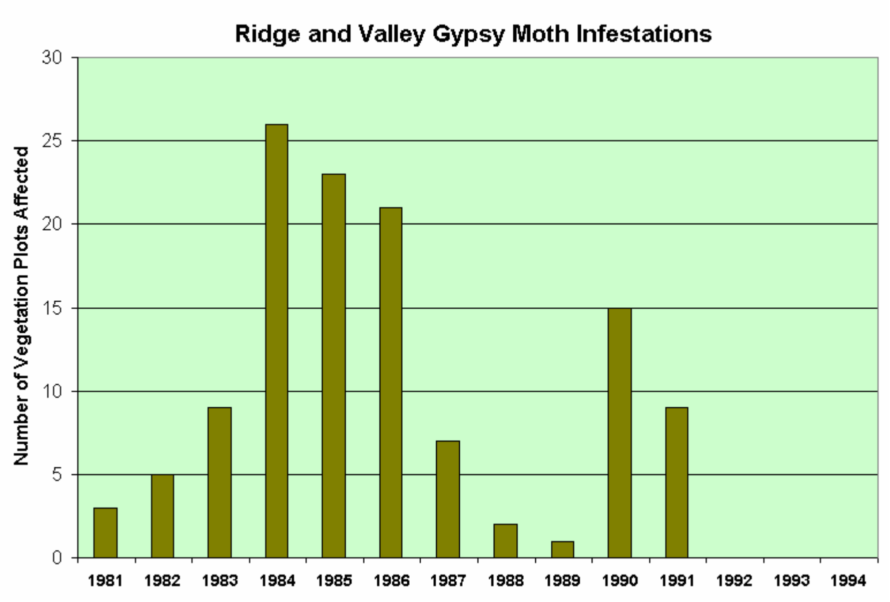
This research was conducted in two study areas that represent the range of environmental conditions present in the central Appalachian highlands: The warmer and drier Ridge and Valley physiographic province, and the cooler and wetter Allegheny Plateau (Figure 1.3). The specific areas were selected to maximize the coverage of public forest or game lands, where development and logging pressure have been less intensive compared to adjacent privately held land. Because of differences in topography, climate, as well as land use and disturbance histories, the forest community composition and structure in the two study areas are dissimilar. Nevertheless, the study areas are in the heart of the geographic range of *K. latifolia* and *R. maximum* (Figures 1.1 and 1.2).

4.2.1 Ridge and Valley Province

This study area is located in western Maryland and south-central Pennsylvania and consists of two large state forest areas – Green Ridge State Forest (GRSF) and Buchanan State Forest (BSF). The majority of the evergreen understory vegetation found in this study area is located in BSF, with the largest concentration located in an area known as the Martin Hill Wild Area, wherein the forests were originally harvested in the late 1800s and early 1900s. The area that is now GRSF in Maryland has had an eventful land use history, as it was cut for timber, tanbark, and hoop poles between 1879 and 1910, and wildfires were common in the regenerating forest for a number of years thereafter (Mash 1996). In the early and middle of the 20th century, this area was planted in fruit (primarily apple) orchards (Mash 1996). The GRSF area now lacks significant coverage of evergreen understory communities. Yearly average minimum and maximum temperatures for this study area are 2.3 and 15.8°C, with temperatures rarely exceeding 32°C in the summer months, but regularly dipping below –10°C in the winter (Stone and Matthews 1974). Elevation ranges from 123 to 845 meters, with steep northeast-southwest trending ridges in the GRSF and a larger contiguous upland area in the Martin Hill section of the BSF. Severe drought – as defined by an average PDSI value of –3.0 or lower over the growing season months of April to September – has occurred seven times since 1900 in the Ridge and Valley study area. The temporal pattern of annual water availability as represented by growing season PDSI averages can be seen in Figure 2.1. Two major waves of gypsy moth infestation have occurred in this study area; one occurring between 1983 and 1987, and another in 1990-1991 (Figure 4.2).

4.2.2 Allegheny Plateau Province

As with the Ridge and Valley, this study area was largely cut in the 20th century, but much of this area has been designated as state forests in the interim, and has undergone a



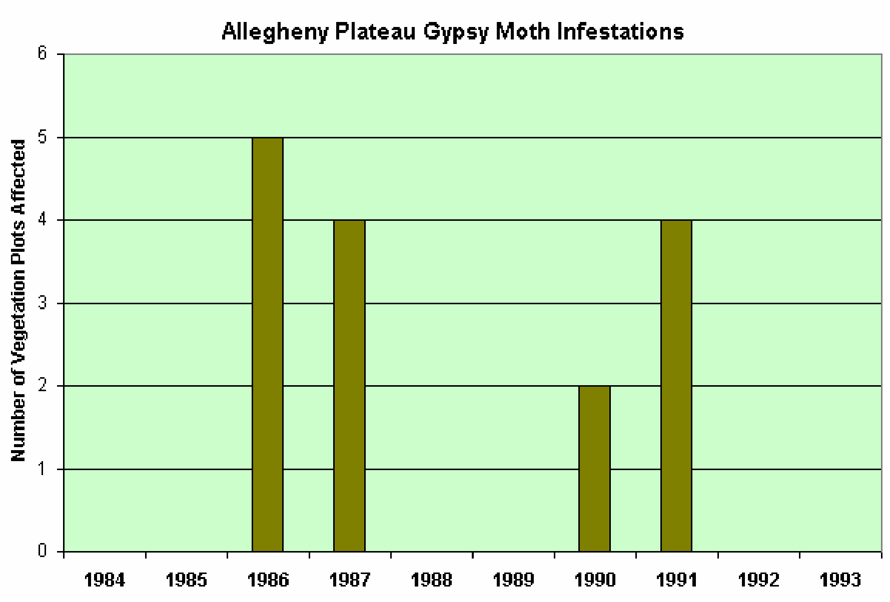


Figure 4.2: Bar charts showing the timing and pervasiveness of intermittent gypsy moth infestations that occurred in the Ridge and Valley and Allegheny Plateau provinces from 1981 through 1991 (based on GIS data from MD and PA Departments Agriculture, Division of Pest Management). The height of the bars related to the number of vegetation plots used in this research that were affected by gypsy moth infestation that year.

decrease in logging pressure as a result. The forest canopy in this study area is primarily deciduous with localized areas dominated by hemlock and other conifers (*Pinus resinosa*, *Pinus strobus*, *Picea abies*, *Larix laricina*, and *Pinus sylvestris*) established in plantations during the 1940s following state acquisition of this area (Continuous Forest Inventory, unpublished data). American chestnut was an important component of these forests previous to its extirpation in the early to mid 20th century due to the blight caused by the fungus *Cryphonectria parasitica* (Braun 1950). The elevation range for the Allegheny Plateau is 304-986 meters, with a humid continental climate characterized by severe winters and mild summers. Severe drought as defined by PDSI growing season averages occurred four times since 1900 in the Allegheny Plateau study are (Figure 2.1). Two major waves of gypsy moth infestation have occurred in this study area: The first in 1986-1987 and the second in 1990-1991 (Figure 4.2).

4.3 Methods

4.3.1 Temporal Dynamics of Evergreen Understory Communities

The goal of the remote sensing change detection was to track the trajectories of *K. latifolia*- and/or *R. maximum*-dominated evergreen understory community growth vigor over time and compare these trajectories with the timing of climatic fluctuations (drought periodicity) and the advent of the major waves of gypsy moth infestation. This study will identify regional patterns of evergreen understory variability in the context of examining its potential to inhibit canopy tree seedling regeneration. It is hypothesized that *K. latifolia* and *R. maximum* are persistent in locations where they currently exist, but vary in their growth vigor (or leaf area) over time. If decreases occur in the growth vigor of

K. latifolia and/or *R. maximum* in response to climatic fluctuations or gypsy moth disturbance, these can be seen as providing periodic openings in the regeneration bottleneck caused by these species. This permits canopy trees regeneration and suggests a driver that prevents forests of the Appalachian highlands from reverting wholesale into shrublands.

Change detection analyses were applied: 1) on the landscape scale using remote sensing; and 2) on a plot-level scale using dendrochronology. The remote sensing analysis employed change vector analysis (CVA, Lambin and Strahler 1994) of the tasseled cap brightness, greenness, and wetness components derived from a time series of Landsat TM image data. The dendrochronology methods employed growth ring measurements from stem sections harvested from numerous *K. latifolia* and *R. maximum* individuals in both study areas.

Drought periodicity on the county level was represented using monthly calculations of the Palmer drought severity index (PDSI, Palmer 1965), which were averaged over the growing season months of April through September. The PDSI is standardized to local climatic conditions, and combines temperature and rainfall data into one number to represent long-term drought over a period of several months. PDSI values between +2 and –2 indicate normal hydrological conditions, and drought conditions are present when PDSI values are lower such that –4.0 or less indicates extreme drought conditions, –3.0 to –3.9 indicates severe drought, and –2.0 to 2.9 represents moderate drought (NOAA Drought Information Center (www.drought.noaa.gov) 2003). Since 1900, moderate to severe droughts have occurred 13 times in both the Ridge and Valley and Allegheny Plateau study areas (Figure 2.1). Data on the spatial extent and temporal return intervals of gypsy moth infestation were obtained from the Pest Management Bureaus of the Pennsylvania and Maryland Departments of Agriculture. This information came in the form of digitized maps of yearly infestation extent, which were initially sketched onto topographic maps during aerial surveys in both states. The most severe gypsy moth infestations occurred in the mid 1980s and early 1990s (Figure 4.2).

4.3.2 Landscape Level Remote Sensing Change Detection

Remote Sensing Change Detection

Indirect methods of change detection in forested landscapes using remote sensing data are numerous (see Singh 1989 and Yuan *et al*. 1998 for reviews). Vegetation indices have frequently been used to assess changes in the composition (Lyon *et al*. 1998) and health (Royle and Lathrop 1997) of vegetation communities. In addition, principal components have been found useful in tracking the progress and net effects of forest defoliation over time (Muchoney and Haack 1994). In his review of several change detection techniques, Singh (1989) categorizes remote sensing change detection into two types of approaches: Those involving the classification of the input data (‘delta-categorical’) and those that utilize the radiometric change between acquisition dates. Change vector analysis (CVA) fits into the latter category, and has been used to describe temporal change in multispectral remote sensing data in terms of both change magnitude and direction in multidimensional space (Lambin and Strahler 1994, Johnson and Kasischke 1998, Townsend *et al*. 2004). Moreover, it has been shown that the results of this technique are enhanced by using the Landsat TM Tasseled Cap components of brightness, greenness, and wetness (Kauth and Thomas 1976, Crist and Ciccone 1984) to describe subtle changes in the growth vigor of forest communities (Allen and Kupfer 2000, 2001). The loss of vegetation or leaf area is characterized by an increase in Tasseled Cap brightness and a decrease in greenness using this approach, whereas an increase in greenness (decrease in brightness) indicates an increase in growth vigor.

For this research, the CVA approach was used to address the underlying hypothesis that the evergreen understory layer is persistent, but variable in growth vigor over time in response to dynamic environmental conditions caused by drought pressure and insect defoliation. Whereas 'delta-categorical' approaches provide a straightforward method for tracking land cover change over time, they are insensitive to more subtle changes in the condition of vegetation communities that remain intact over time. A hybrid approach was employed in this research in which the forest evergreen understory community types were classified, then changes in these communities over time were examined using a CVA technique wherein changes over time in the angular direction of change were examined in the Tasseled Cap greenness – brightness plane (see Figure 4.3).

Image Data Acquisition

The landscape perspective on changes in the growth vigor (leaf area or density) of evergreen understory communities was obtained using a time series of Landsat TM images obtained from 1984 – its first year of data collection – until 2000. Five Landsat images were used in the Allegheny Plateau and four images in the Ridge and Valley

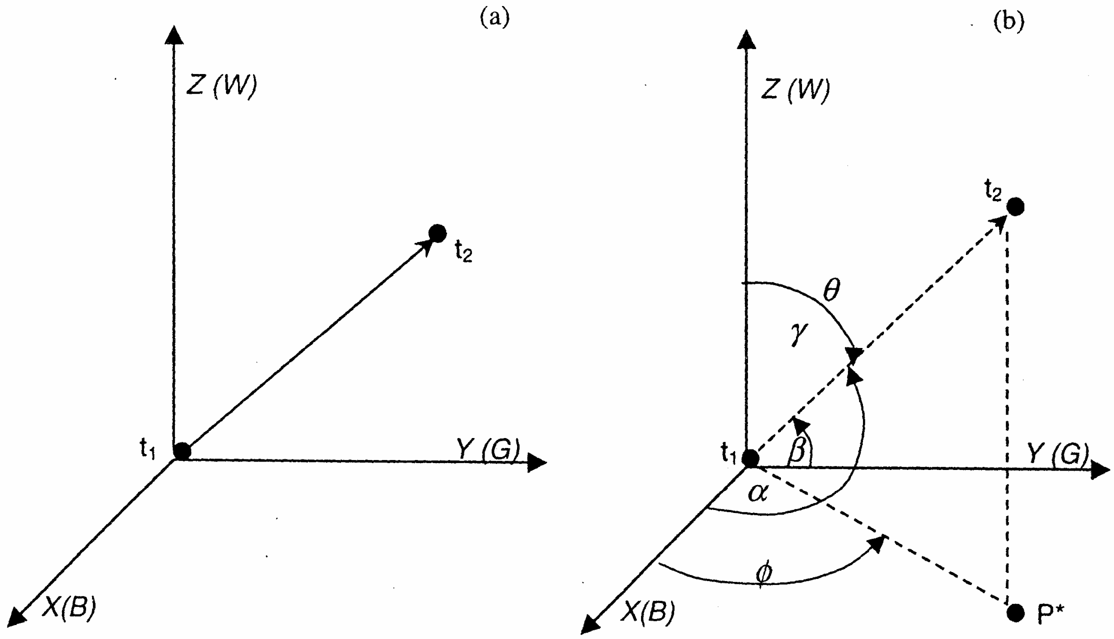


Figure 4.3: Schematic diagram of the theoretical framework of change vector analysis (CVA, from Allen and Kupfer 2000). The point denoted as t_1 represents the value of tasseled cap brightness, greenness, and wetness at time 1, whereas as t_2 represents the corresponding value in CVA space at time 2. The length of the line connecting these two points represents the magnitude of the overall change. The angle Φ describes the amount of change over the time period that has taken place on the X-Y (Brightness-Greenness) plane, which is hypothesized to be the axis most correlated with evergreen understory change over time in this research.

study area to track changes in the growth vigor of the evergreen understory layer in these disparate provinces (Table A17). Leaf-off images were employed to track characteristics of evergreen vegetation rather than the deciduous understory. Tasseled Cap brightness, greenness, and wetness components (Crist and Cicone 1984, Crist and Kauth 1986) were created using image data from each date to compare trajectories of *K. latifolia*- and/or *R. maximum*-dominated evergreen understory community growth vigor in areas that experienced dissimilar disturbance regimes (drought and defoliations).

Image Data Pre-Processing

Geometric Correction

The Landsat TM images were geographically referenced to UTM zone 17 NAD 83 coordinates using ground control points (GCPs) that were identifiable on both the image and USGS 1:24,000 scale quadrangle maps in conjunction with nearest neighbor resampling and 2nd order polynomial transformations for reprojection to the new coordintate system. The target average root mean square error (RMSE) was <0.5, indicating a spatial error between the map source and image data of about one half of a 30x30 meter TM pixel (Table A17).

Image Normalization

Accurate detection of actual changes in forest characteristics requires the minimization of differences between the images used in the time series related to extraneous factors such as sun angle, atmospheric transparency, and detector calibration. In addition, the differential influence of topography on solar radiation within each image must be minimized. An empirical topographic normalization technique was applied to the individual Landsat images used in the time series to reduce the influence of differential solar illumination related to topography (Allen 2000). An empirical model relating solar illumination angle (cos(i), computed pixel by pixel from a 30 meter digital elevation model and solar azimuth and elevation values for the Landsat overflight) to differential reflectance of forested pixels was applied band by band such that illumination corrected reflectance (R_i) is calculated as:

$$R_i = R_o - \cos(i) * M - B + R(\mathrm{hat})$$

where M and B are regression parameters, R_o is the original reflectance, and R(hat) is the mean reflectance (Meyer *et al*. 1993). Tables A18 and A19 contain the regression parameters for each image subset for the Allegheny Plateau and Ridge and Valley study areas, respectively.

The use of images acquired on or close to anniversary dates removes a large amount of potential differences between images arising from sun angle and phenological factors (Coppin and Bauer 1996). Other sources of unwanted radiometric differences were removed using an empirical scene normalization technique described in Collins and Woodcock (1996) wherein the 2000 Landsat image served as a base to which the other Landsat scenes were normalized. This method entailed matching invariant bright and dark targets (bright surfaces such as roads or quarries and dark surfaces such as water bodies) on the various scenes and using their spectral data to calculate regression equations on a band-by-band basis to predict the 2000 image digital numbers (DNs) from those in the 1984, 1986, 1991, and 1997 scenes used to perform change detection analysis on the Allegheny Plateau study area evergreen understory communities (Table A20). The same technique was then applied to normalize the 1984, 1992, and 1997 Ridge and Valley Landsat TM images to the 2000 Landsat ETM image (Table A21).

Change Vector Analysis Methods

A tasseled cap transformation was applied to the five normalized images that were used for the Allegheny Plateau time line and the four normalized images that were applied to the Ridge and valley time line using the ERDAS Imagine software. The values were not stretched to 8-bit radiometric resolution when the tasseled cap components were created, but instead all of the brightness, greenness, and wetness components from the image set in each study area were compared to find the minimum and maximum values across all images so that cumulative dynamic range would remain intact. The CVA angular and directional changes and change magnitude were then computed following Townsend *et al*. (2004). CVA was implemented across 1984 and 2000 and in between each successive set of images covering the 1984 – 2000 time span. The analyses were thus for the1984-1986, 1986-1991, 1991-1997, and 1997-2000 for the Allegheny Plateau and 1984-1992, 1992-1997, and 1997-2000 for the Ridge and Valley study area.

GIS Methods

This research employed the land cover classification developed in chapter 3 and a set of topographic indices developed within a GIS (Table A4). The raster thematic land cover map includes classes for *R. maximum*, *K. latifolia*, ‘Mixed’ (*R. maximum* and *K. latifolia*) understory, and ‘Control’ forested areas that do not contain an evergreen understory. GIS masks of *K. latifolia*, *R. maximum* and 'Mixed' evergreen understory were developed to extract a random sample 10 percent of each class for use in the remote sensing change detection analysis in both study areas.

From the GIS data layers, values for the TRMI (an elevation-derived index of relative moisture availability, and therefore potential susceptibility to drought), the total number gypsy moth disturbance years, and the CVA output were extracted for the samples of *K. latifolia*, *R. maximum*, and 'Mixed' understory types. Areas that were one standard deviation below and above the mean TRMI value for each understory type were identified as 'wet' and 'dry', respectively to characterize the degree of drought susceptibility based on topographic position. In the Ridge and Valley study area, regions in which gypsy moth disturbance occurred in only 2 or fewer years in the period of 1981 through 1994 were depicted as having a low amount of gypsy moth infestation, and areas where infestation occurred more than twice were considered to have undergone a high amount of this disturbance. In the Allegheny Plateau, areas were differentiated based on sites that did not experience infestation between 1984 and 1993. Lastly, the angular values of Φ derived from the CVA (Figure 4.3) were also extracted for the locations of all of the understory type sample pixels. The angular direction Φ describes the direction of change on the greenness-brightness plane. In other words, Φ is a measure of angular change relevant changes in the amount of 'greenness' in an area. Based on a comparison of the values derived at the locations of better than 200 evergreen understory vegetation plots, tasseled cap greenness is highly related to NDVI in these study areas ($R^2 = .972$). NDVI has been empirically related to standing green biomass, leaf area index, canopy closure, and growth vigor (Botkin *et al*. 1984, Holben and Tucker 1985, Lambin and Strahler 1994, Price and Bausch 1995).

Because of the inherent non-linearity of the angular Φ value, a Mann-Whitney test was performed on rank ordered data to test for significance in differences of Φ values between topographically dry and wet areas as well as between the high and low gypsy moth infestation areas. The chi-square statistic was used to test for significance in the differences in angular Φ changes that occurred over the individual time periods and over the entire time span (1984 – 2000).

4.3.3 Plot-Level Dendrochronology Methods

Samples of stem wood from *K. latifolia* and *R. maximum* individuals were collected in the two study areas and their annual growth rings measured to quantify patterns in their growth and to test specific hypotheses about the temporal dynamics of their growth vigor. These hypotheses are:

1) Large-scale factors such as climatic fluctuations and stand-wide (exogenous) disturbances (i.e. gypsy moth defoliation) impact the temporal patterns of *K. latifolia* and *R. maximum* growth vigor (big and slow factors). These factors are topographically mediated, in that both drought (Parker 1982, McNab 1993) and gypsy moth disturbance susceptibility (Liebhold *et al*. 1994) are related to topographic position on the landscape scale;
2) Temporal dynamics of growth vigor also vary over small spatial scales in evergreen understory layer communities as an integrated response to small-scale

endogenous disturbances such as tree- and limb-fall, sunfleck variations in the understory, and subsequent changes in inter- and intraspecific competition (small and fast factors); and

3) These factors occurring at different temporal and spatial scales combine to produce the temporal and spatial patterns in growth vigor of evergreen understory communities that are detectable at an intermediate scale using remote sensing.

In a broad sense, the signal of the large scale factors must be discriminated from the noise that characterizes the year-to-year variation due to the stand-scale endogenous variables.

Stem wood discs from 331 *R. maximum* and *K. latifolia* stems were collected from the Ridge and Valley and Allegheny Plateau study areas, to validate the patterns of growth vigor apparent in the remote sensing change detection analysis and to examine the behavior of *K. latifolia* and *R. maximum* individuals that make up these patterns. As with the remote sensing analysis, sample selection was stratified using TRMI to capture a representative sample of drought stress conditions and level of gypsy moth disturbance. This yielded data from 19 plots in the Ridge and Valley (7 dry, 9 wet, 10 defoliated) and 27 plots in the Allegheny Plateau (6 dry, 6 wet, 8 gypsy moth). Stem wood was harvested at approximately 30 cm above the forest floor (*sensu* McGee and Smith 1967) from shrubs that were widely spaced along the 60 meter transects to minimize spatial autocorrelation between the individual stems.

The harvested wood samples were cut into discs of a standard length of approximately 1.25 cm. They were then sanded and polished to facilitate the discrimination of annual growth rings using the following sequence of sanding grits: 60,120, 220, 320-coarse, 320-fine, 400, 600, 1800, and 2400. The growth rings were measured in the thickest direction from the center of the disc to maximize the discernability of the growth rings and to minimize the measurement of growth ring compression caused by stem bending. Both *K. latifolia* and *R. maximum* stems tended to show non-symmetric growth from the center in response to stem bending during shrub growth, as *R. maximum* and *K. latifolia* are bombarded by tree- and limb-falls during their development (Wilson 1997). The MeasureJ2X software (Voortech 2001) was used to organize the growth increment data and as an interface among the various hardware. An Olympus S260 stereoscope connected to a Sony Trinitron video monitor was used to view the growth increments from the sanded stems, which were mounted on a Velmex single axis UniSlide platform.

The annual growth rings were more discernable in *R. maximum* than *K. latifolia*. This likely due in part to differences in the growth habits of these two species, as *R. maximum* leaves are not photosynthetically active during the winter whereas *K. latifolia* are active during warm winter days (Nilsen 1992). During mild winters, *K. latifolia* may be able to grow throughout the year, and a terminal boundary will not be apparent to mark the end of the growth year. The difficulty of discerning annual growth increments in *K. latifolia* is confounded by its slow growing habit.

An analysis of tree ring series depends on maximizing the signal to noise ratio in the data. To accomplish this, the biological growth curve signal of the individual species must be separated from signals produced by macroclimate, localized disturbances, and exogenous factors that influence vegetation at the stand level (Graybill *et al.* 1982, Cook 1990b). Tree ring series contain expressions of several environmental signals that are usually conceptualized as a linear aggregate, that is:

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t$$

Where:

R_t is the observed ring-width series;

A_t is the biological growth curve signal, which is age-size related;

C_t is the macroclimatic signal common to all individuals sampled at a site;

$D1_t$ is the signal related to local endogenous disturbances;

$D2_t$ is the signal related to stand-wide exogenous disturbance; and

E_t is the random growth signal of year-to-year variability not related to the other signals.

There is a considerable amount of noise in the growth ring record of the evergreen understory shrub species *K. latifolia* and *R. maximum*. Most tree ring research focuses on the growth records of canopy trees, whereas shrubs and understory woody plants are not commonly analyzed (but see Pornon and Douche 1995). Growth increments on canopy trees are not affected by the gravity-related disturbances such as tree- or limb-fall events that may greatly influence understory trees or shrubs. In addition, the evergreen habit of *K. latifolia* and *R. maximum* expose their leaves to winter injuries during harsh winters. Finally, the small-scale spatial variability of microsite conditions in the forest understory further obfuscate exogenous signals from macroclimatic signals or exogenous disturbances that are expected to be present in all growth ring series from a given site. Separating large-scale signals from site factors occurring at the scale of the individual shrub is therefore quite challenging.

Estimation of the biological growth trend (A_t) and the periodic releases and suppressions of the *K. latifolia* and *R. maximum* individuals collected for this study followed methods well established in the literature. First, the DOS program COFECHA (Grissino-Mayer *et al*. 1997) was employed to determine whether the growth rings of individuals collected on each plot were similar enough to permit crossdating based on common growth patterns. Crossdating is typically successful in canopy tree ring series collected at a common site and is based on the theory that the macroclimatic signal and/or exogenous disturbance signals are emergent in the growth ring series. Following that, biological growth trends (A_t) in the increment data were calculated as fourth order polynomial trend lines (Cook 1990b) for all of the individual samples. These curves represent the generalized growth trajectories of individuals, and minimize year-to-year 'noise' caused by small-scaled disturbances such as by tree- and limb-falls. These general trend lines in *R. maximum* and *K. latifolia* individuals were then examined to identify the timing of high and low points in their overall growth rates and to detect correspondence with the timing of gypsy moth defoliations and drought fluctuations.

The DOS program JOLTS (Grissino-Mayer *et al*. 1997) was used to identify suppressions and releases in the annual growth increment data based on a running mean of 5 years prior to a release or suppression event and 3 years afterwards. To qualify as a suppression or release, the event had to differ by at least a factor of 1.5 from the prior and posterior running mean. No minimum temporal period was set to limit how often a release or suppression could be detected by the program on a growth ring series, although the occurrence of an event necessarily changed the running means, thereby affecting the reporting frequency of events. Comparisons were then made between the timing of peaks in the number of individuals that experienced ephemeral growth suppressions or releases and the timing of gypsy moth defoliations and drought events to identify factors influencing individual and stand growth patterns.

4.4 Results

4.4.1 Landscape Scale Changes

The landscape level change detection analysis indicated significant relationships in the spatial patterns of changes in growth vigor over time based on topographically mediated drought stress and the distribution of gypsy moth defoliation in both the Ridge and Valley and the Allegheny Plateau provinces. Moreover, these relationships are temporally consistent with the timing of drought events and gypsy moth disturbances in both study areas. Results from the various evergreen understory community types, disturbance types, and physiographic provinces will be discussed in turn.

In the Ridge and Valley province, a significant difference in *K. latifolia* growth vigor change as a function of gypsy moth infestation was noted for the 1984-2000 time span (df 1/6366, $\chi^2 = 6.18$, $p = .013$), with areas experiencing a lower number of infestation years exhibiting significantly higher amount growth vigor by the end of that time period (Figure 4.4). However, a significantly larger increase in growth vigor is apparent in high infestation regions during the period when the infestation would have been occurring (1984-1992), and continued between 1992 and 1997. The significantly greater shift away from greenness between 1997 and 2000 (df 1/6513, $\chi^2 = 9.66$, p = .002) coincides with the drought year of 1999 (PDSI < -3) in the Ridge and Valley province, and may be an artifact of the spatial autocorrelation between topographically dry areas and the dry oak communities that gypsy moths favor (Liebhold *et al*. 1994). This period of greater 'browning down' may also have contributed to the significantly lower growth vigor reported in higher gypsy moth infested areas between 1984 and 2000. There were also significantly higher shifts towards greenness for the 1984-1992 and 1992-1997 time periods in topographically dry areas – during a period that lacked a drought year – followed by a significantly greater browning down in the drier areas during the 1997-2000 time frame.

R. maximum in the Ridge and Valley also showed a significantly higher growth vigor spurt as a function of gypsy moth activity level that was associated with infestation timing (Figure 4.5). In addition, *R. maximum* growing in topographically drier areas indicated a significantly different shift towards greenness during the three individual time periods examined. The latter result raises a possible question: was *R. maximum* expanding or becoming denser in areas upslope from its core areas close to streams?

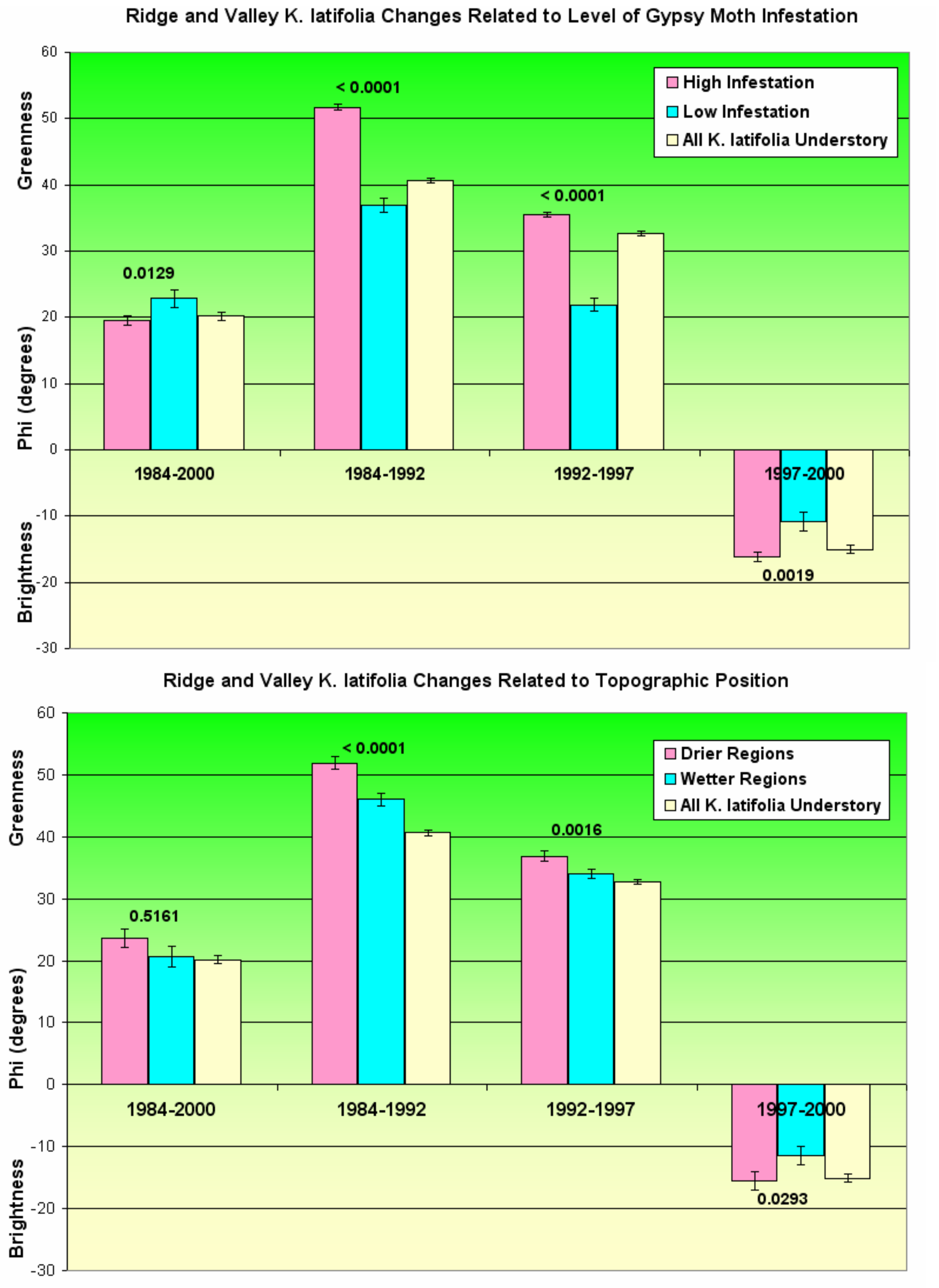
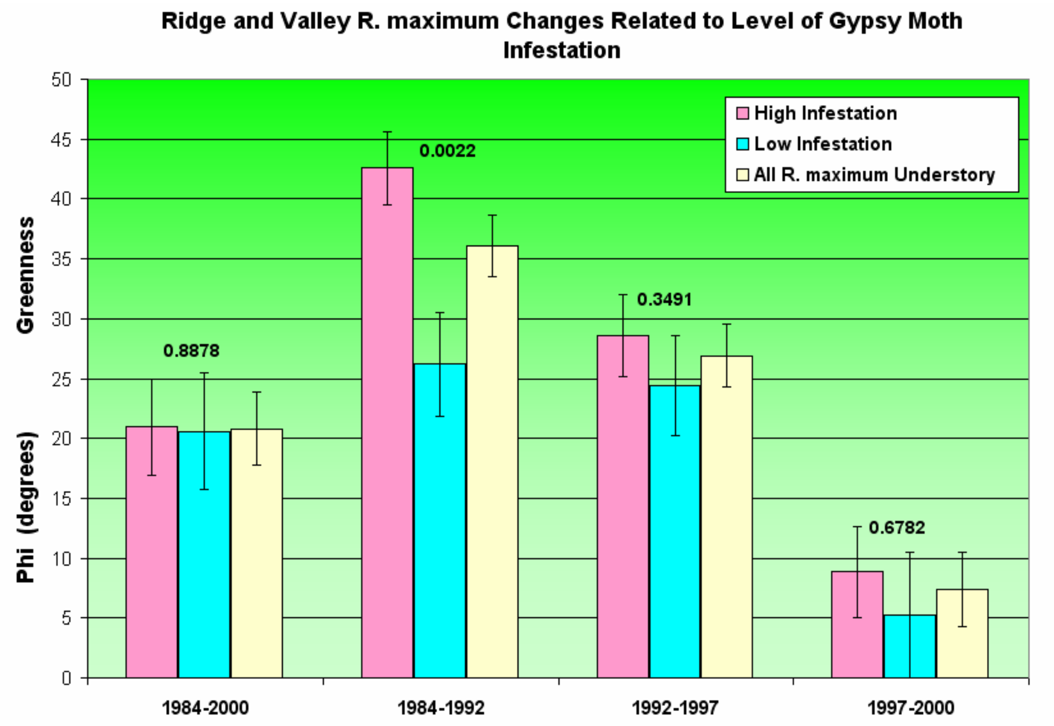
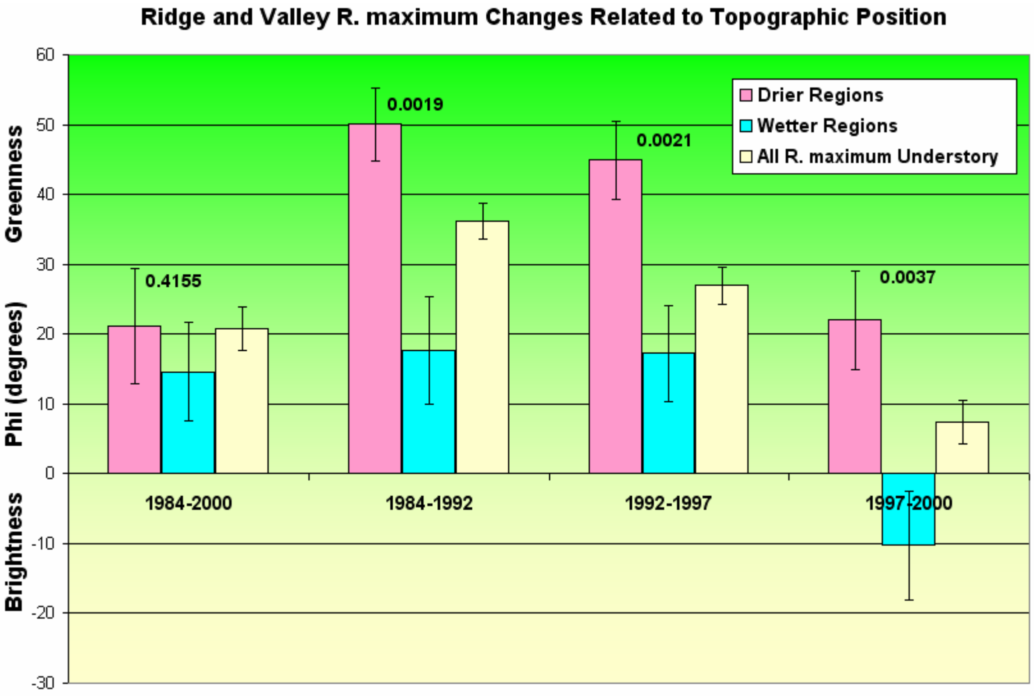


Figure 4.4: Results from the change vector analysis of the remote sensing data in *K. latifolia* regions in the Ridge and Valley study area. Bars positioned above the x-axis indicate an increase in greenness and those below the x-axis indicate an increase in brightness, or a decrease in greenness in the indicated category. Statistical significance in differences was assessed using the chi-square statistic obtained from the Mann Whitney test on rank-ordered data.



Ridge and Valley R. maximum Changes Related to Level of Gypsy Moth Infestation



Ridge and Valley R. maximum Changes Related to Topographic Position

Figure 4.5: Results from the change vector analysis of the remote sensing data in *R. maximum* regions in the Ridge and Valley study area. Bars positioned above the x-axis indicate an increase in greenness and those below the x-axis indicate an increase in brightness, or a decrease in greenness in the indicated category. Statistical significance in differences was assessed using the chi-square statistic obtained from the Mann Whitney test on rank-ordered data.

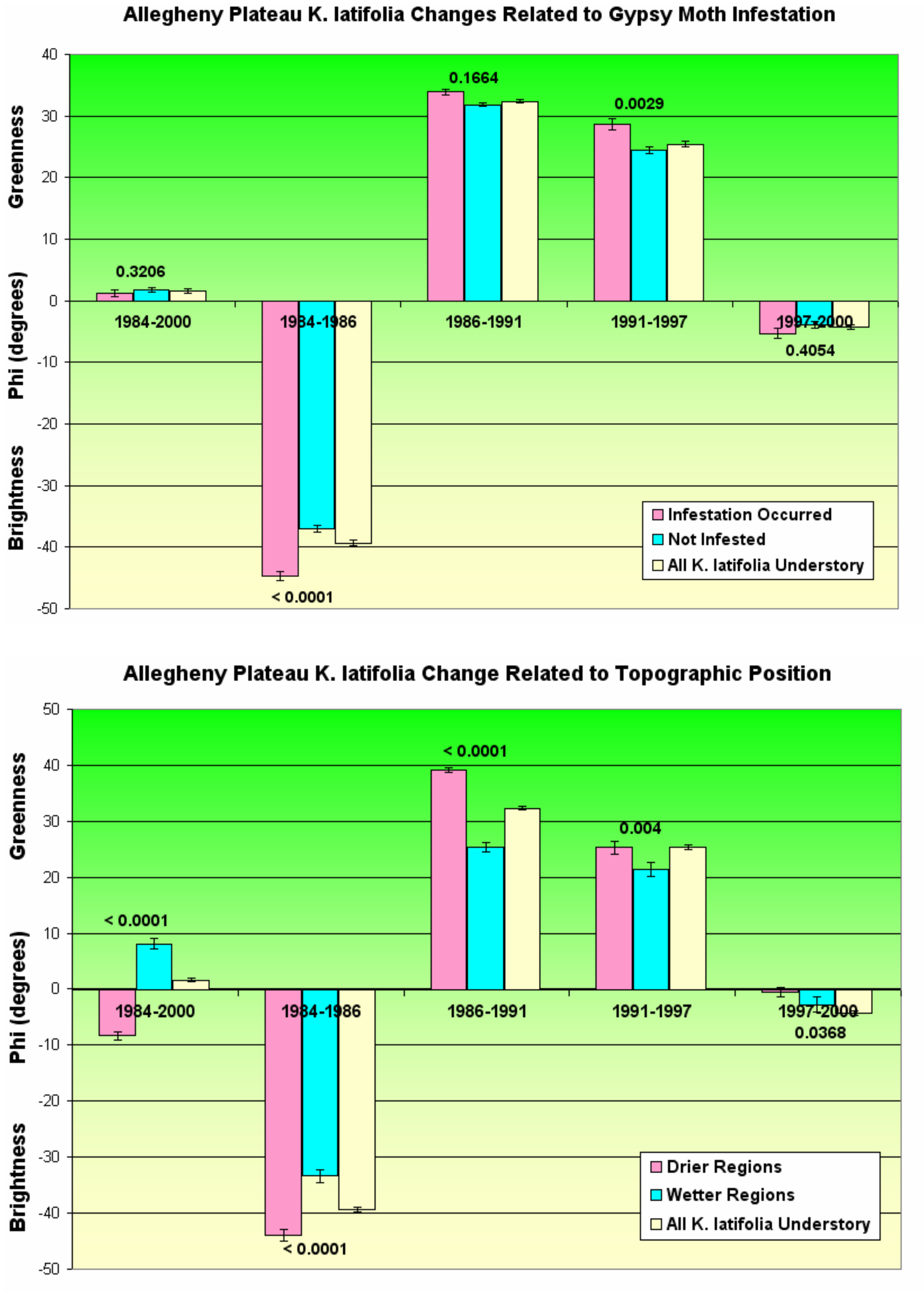


Figure 4.6: Results from the change vector analysis of the remote sensing data in *K. latifolia* regions in the Allegheny Plateau study area. Bars positioned above the x-axis indicate an increase in greenness and those below the x-axis indicate an increase in brightness, or a decrease in greenness in the indicated category. Statistical significance in differences was assessed using the chi-square statistic obtained from the Mann Whitney test on rank-ordered data.

All of the *K. latifolia* categories in the Allegheny Plateau province showed an unequivocal shift towards brightness between 1984 and 1986 (Figure 4.6). This may in part be due to a phenological inconsistency captured by the early Landsat TM image acquisition date in 1986. The 1984 Landsat image was acquired on April 12 and the 1986 image was acquired on March 24, potentially before the emergence of new leaves on *K. latifolia* and *R. maximum*, which occurs at the beginning of the growing season. The brightness shift was magnified in the *K. latifolia* compared to the *R. maximum* (see Figure 4.8), which lends credence to this hypothesis, because *K. latifolia* obtains half of its leaves anew every spring, compared to about 20 percent for *R. maximum* (Monk *et al*. 1985). In addition, it is also reasonable that drier, more exposed, and gypsy moth susceptible *K. latifolia* plots showed a net shift towards brightness between 1984 and 1986, because such sites lag slightly in terms of phenology in the spring. Discarding the 1984-1986 analyses, it appears that topography was a more significant gradient in explaining changes in image-derived growth vigor compared to gypsy moth in the Allegheny Plateau (Figure 4.6, also see Figures 2.1 and 4.2). Significant differences existed between wet and dry areas in all of the time periods for *K. latifolia*, although a slightly more significant net greening did occur in gypsy moth infested areas during 1991-1997 (following defoliation). Overall, topographically wetter areas exhibited a net shift towards greenness compared to a net shift towards brightness in dry areas between 1984-2000, but the dry areas exhibited significantly higher shifts towards greenness during each of the 1986-1991 and 1991-1997 time periods.

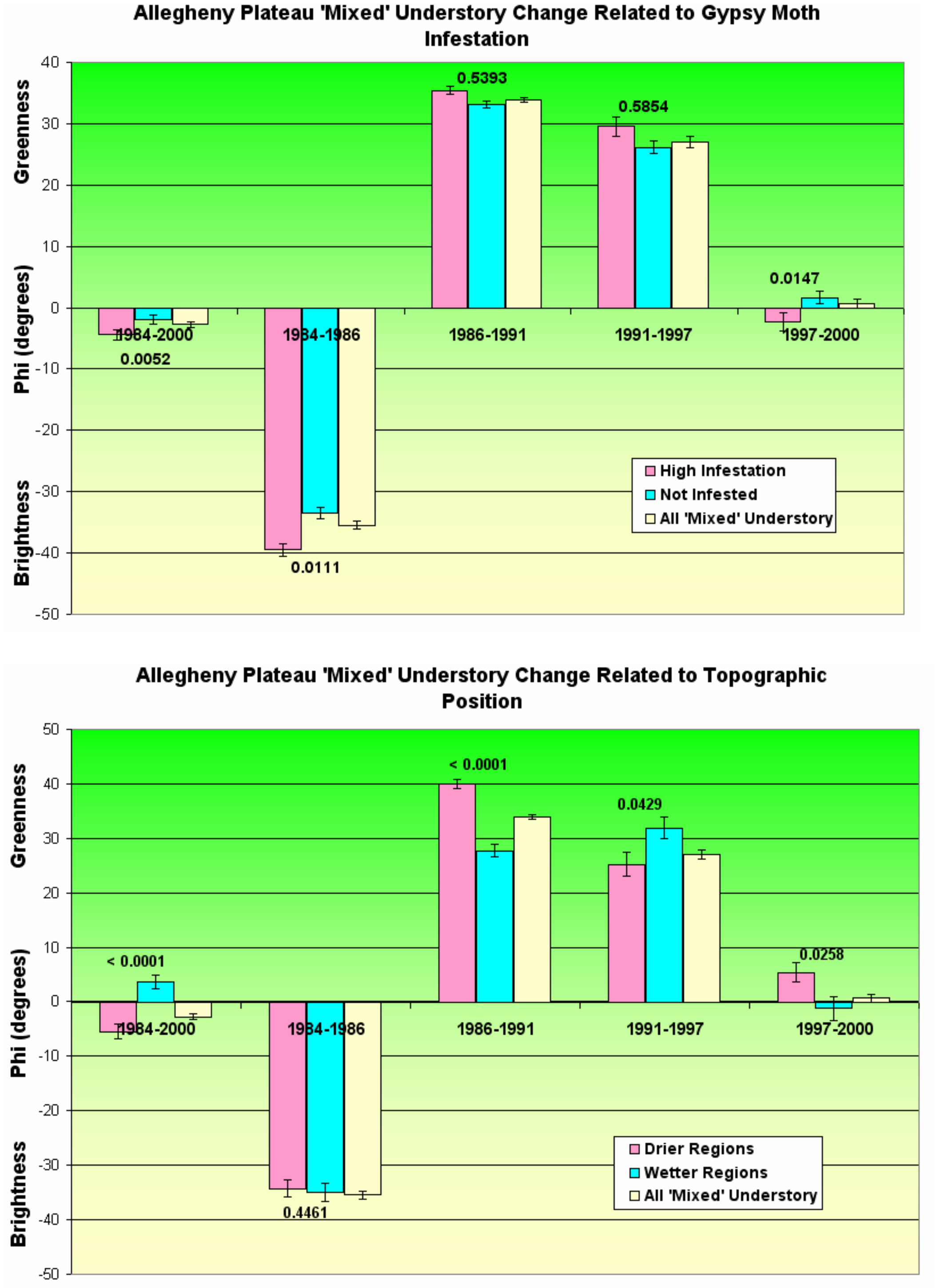


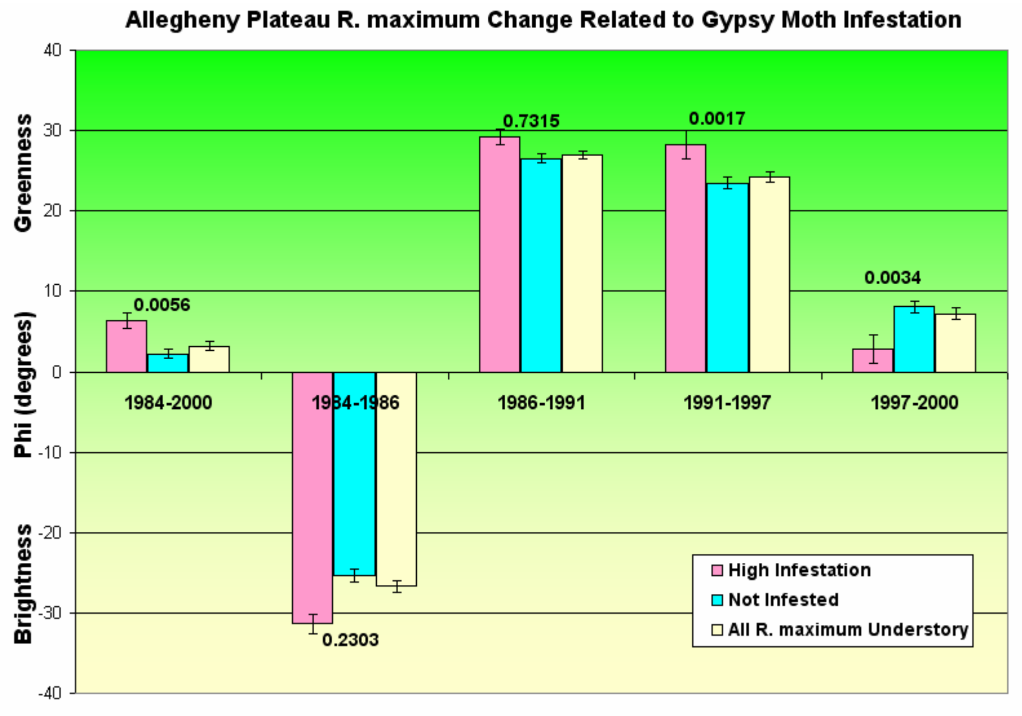
Figure 4.7: Results from the change vector analysis of the remote sensing data in ‘Mixed’ (*K. latifolia* and *R. maximum*) regions in the Allegheny Plateau study area. Bars positioned above the x-axis indicate an increase in greenness and those below the x-axis indicate an increase in brightness, or a decrease in greenness in the indicated category. Statistical significance in differences was assessed using the chi-square statistic obtained from the Mann Whitney test on rank-ordered data.

As with *K. latifolia*, gypsy moth infestation apparently was not as important as topographically mediated drought stress in terms of growth vigor changes in the 'Mixed' evergreen understory communities (Figure 4.7). Drier areas showed a significantly higher shift towards greenness during the 1986-1991 time period (no drought). However, drier 'Mixed' evergreen understory areas are similar to *R. maximum* areas in that they were significantly lower in their shift towards greenness during the 1991-1997 time period (three years of moderate to severe drought). This is consistent with the interpretation that the tasseled cap greenness component responds to a combination of the responses from both species.

Significantly larger net increases in greenness occurred in the wetter *R. maximum* areas compared to drier areas (Figure 4.8) during 1984-2000, a period characterized by moderate to severe drought years. Interestingly, affected *R. maximum* areas responded to gypsy moth defoliation (1984-2000 and 1991-1997 periods) with a significantly higher shift towards the CVA greenness axis (Figure 4.8). In addition, *R. maximum* understories exhibited a significantly higher overall shift towards greenness in dry areas during the 1986-1991, but had a significantly lower shift in that direction in the droughty 1991-1997 period. This suggests that marginal *R. maximum* areas green up and brown down rapidly in response to climatic conditions.

4.4.2 Plot Scale Changes

The individual patterns in the growth ring increments of the *K. latifolia* and *R. maximum* individuals harvested for this study suggest that the temporal component of growth vigor



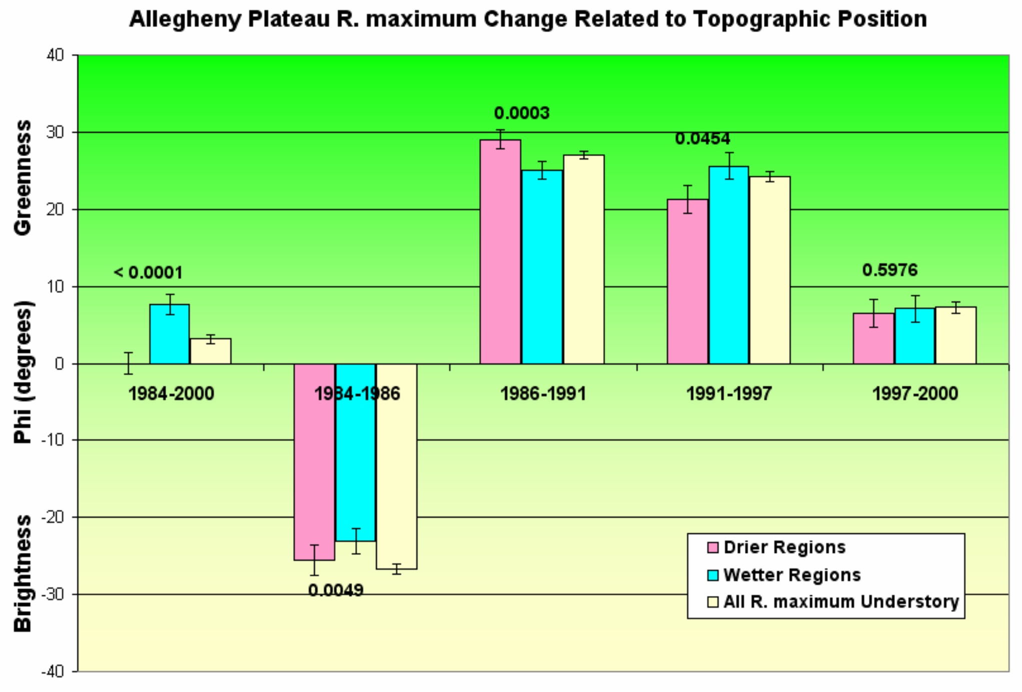


Figure 4.8: Results from the change vector analysis of the remote sensing data in *R. maximum* regions in the Allegheny Plateau study area. Bars positioned above the x-axis indicate an increase in greenness and those below the x-axis indicate an increase in brightness, or a decrease in greenness in the indicated category.

was especially sensitive to microsite conditions in the forest understory. However, the data also indicate relationships between growth and climatic fluctuations and/or gypsy moth disturbance. The individualistic nature of growth vigor patterns in the harvested *R. maximum* and *K. latifolia* was apparent from a failed attempt to build a chronology within individual sites from which stem wood was harvested for analysis. No meaningful correlations were identified when cross-dating the tree ring the tree ring series by site using the COFECHA program (Grissino-Mayer *et al*. 1997). Cross-dating is generally successful only when growth rings are from trees (especially canopy trees) that experienced similar growing conditions (Graybill *et al*. 1982, Cook 1990b). However, multiple factors (sudden disturbance or removal of competition) can affect individual trees differently, leading to anomalous ring growth and preventing correlation among ring series. This appears to be the case for understory woody vegetation such as *K. latifolia* and *R. maximum*, in which individual-specific microsite differences in growing conditions produce uncorrelated growth increments on a given plot. The difference in the growth trends typical of a relatively undisturbed canopy tree with low competition and those of *K. latifolia* and *R. maximum* individuals harvested for this study is readily apparent (Figure 4.9).

Despite some of the limitations in the data, the dendrochronological analyses produced several important results. First, the average stem diameter growth rate for *K. latifolia* was identical in both the warm and dry Ridge and Valley and the cool and wet Allegheny Plateau. Linear regression of stem diameter with age (y-intercept constrained to 0) indicated identical slopes for individuals harvested in the two provinces (Figure 4.10). In

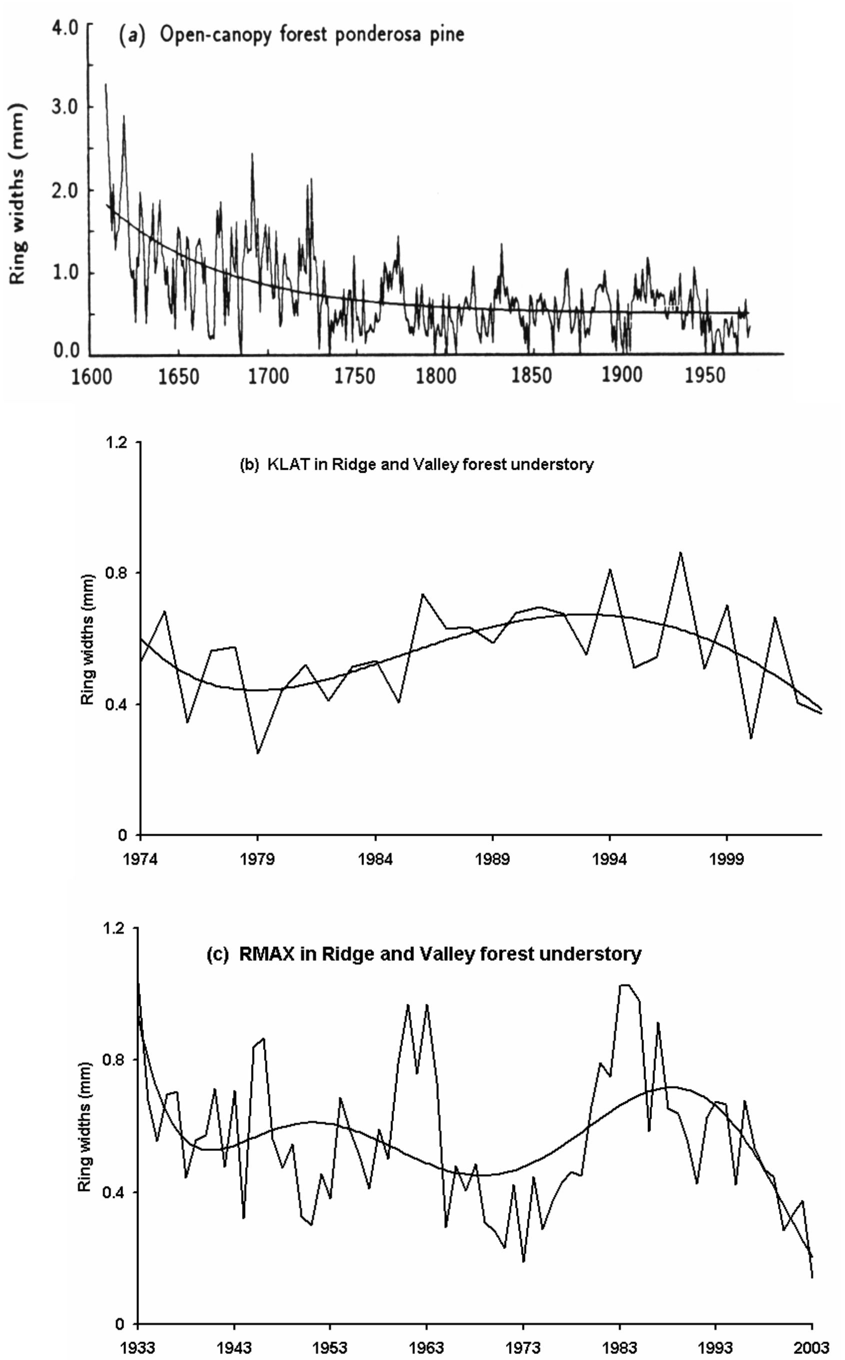


Figure 4.9. Examples of typical growth trends found in tree ring data. Series (a) is from a ponderosa pine growing in a semiarid environment (Cook 1990b), series (b) is from a *K. latifolia* (KLAT) individual growing in the understory of an Eastern U.S. temperate forest in the central Appalachian Mountains, and series (c) is from a *R. maximum* (RMAX) growing in a similar forest understory environment. Series (a) exhibits the classic exponential decay growth trend of a tree that experiences minimal competition and disturbance, and (b) and (c) suggest how disturbance and competition can modify that trend pattern in a woody understory plant.

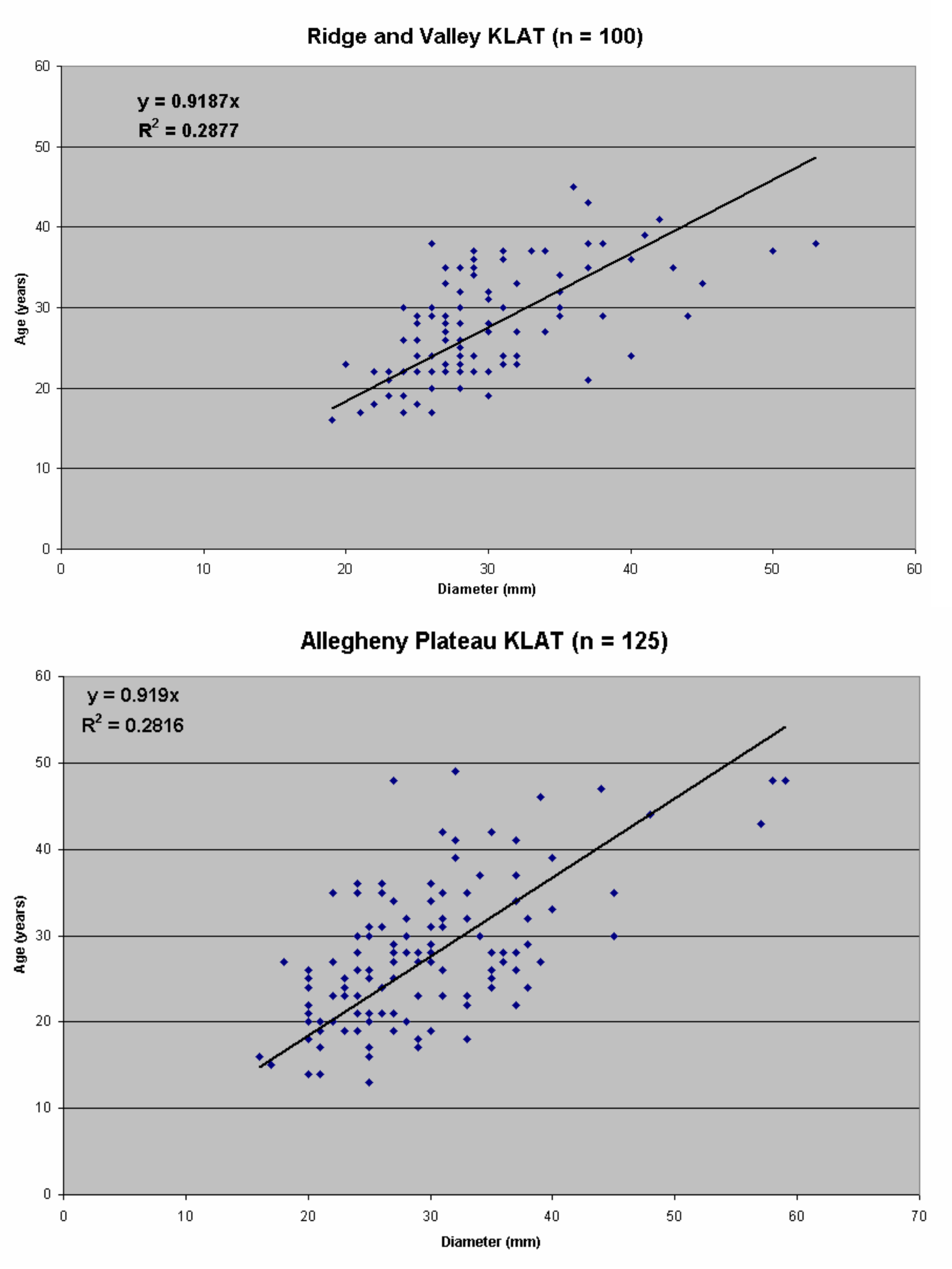


Figure 4.10: Relationship between age and stem diameter of *Kalmia latifolia* in the warmer and drier Ridge and Valley province and the cooler and wetter Allegheny Plateau province. Note the similar regression slope. *Y*-intercepts were constrained to be 0.

addition, *K. latifolia* shows no signs of inhibited growth when located in a significantly drier macroclimatic environment. On the other hand, the aggregate growth pattern for the moisture-loving *R. maximum* showed the expected result that individuals located in the cooler, wetter Allegheny Plateau grew at a faster rate than those harvested from the Ridge and Valley province, albeit only by a small margin (Figure 4.11). The relatively low R^2 value obtained for *K. latifolia* and *R. maximum* demonstrate the individualistic nature and high variability of the growth trajectories of these species. The mean stem diameter for *K. latifolia* was 3.01cm (n=100, *s* =.38) in the Ridge and Valley and 2.97cm (n=125, *s* =.61) in the Plateau study area. The mean stem diameter for *R. maximum* was 5.37cm (n=9, *s* =1.02) in the Ridge and Valley and 4.02cm (n=68, *s* =1.11) in the Plateau study area. The yearly changes in growth vigor were interpreted using the biological growth curves and the instances of suppression and release in the harvested individuals. For comparison, individuals from dry and gypsy moth infested plots were considered stressed, whereas wet and non-infested individuals were considered not stressed. The instances of peaks and lows in the growth trends and the timing of suppressions and releases were subsequently compared to the timing of gypsy moth defoliation and climatic fluctuations. Through this approach, the divergent individual responses in the growth ring series were maintained (i.e. no averaging was applied).

In the Ridge and Valley dry *K. latifolia* plots, the peaks of the biological growth trends converged in 1992 and again in 1996 through 1998, all of which were favorable years in terms of moisture availability (Figure 4.12). A peak also occurred in 1984, coinciding with a small amount of gypsy moth activity in two of the plots from which these growth

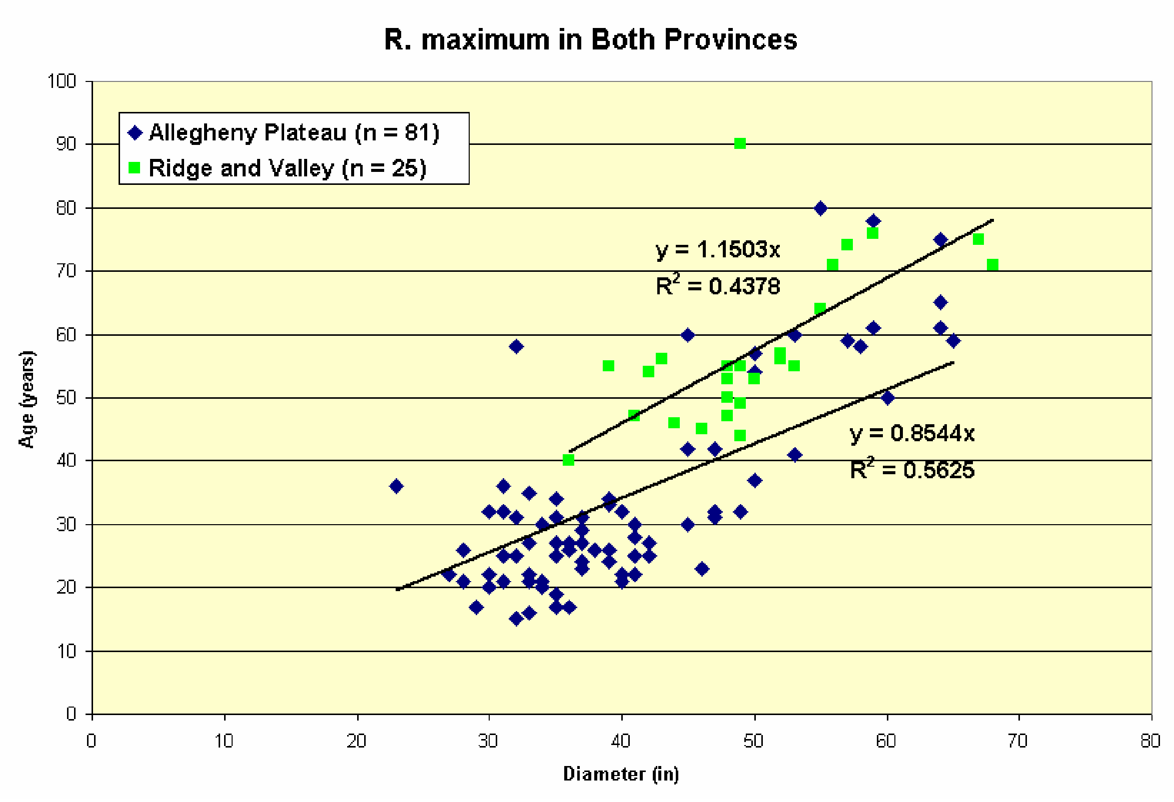


Figure 4.11: Relationship between age and stem diameter of *Rhododendron maximum* in Ridge and Valley province and the Allegheny Plateau province. The slopes of the regression equations indicate that growth trends are somewhat more rapid on the cooler and wetter Allegheny Plateau than the warmer and drier Ridge and Valley region.

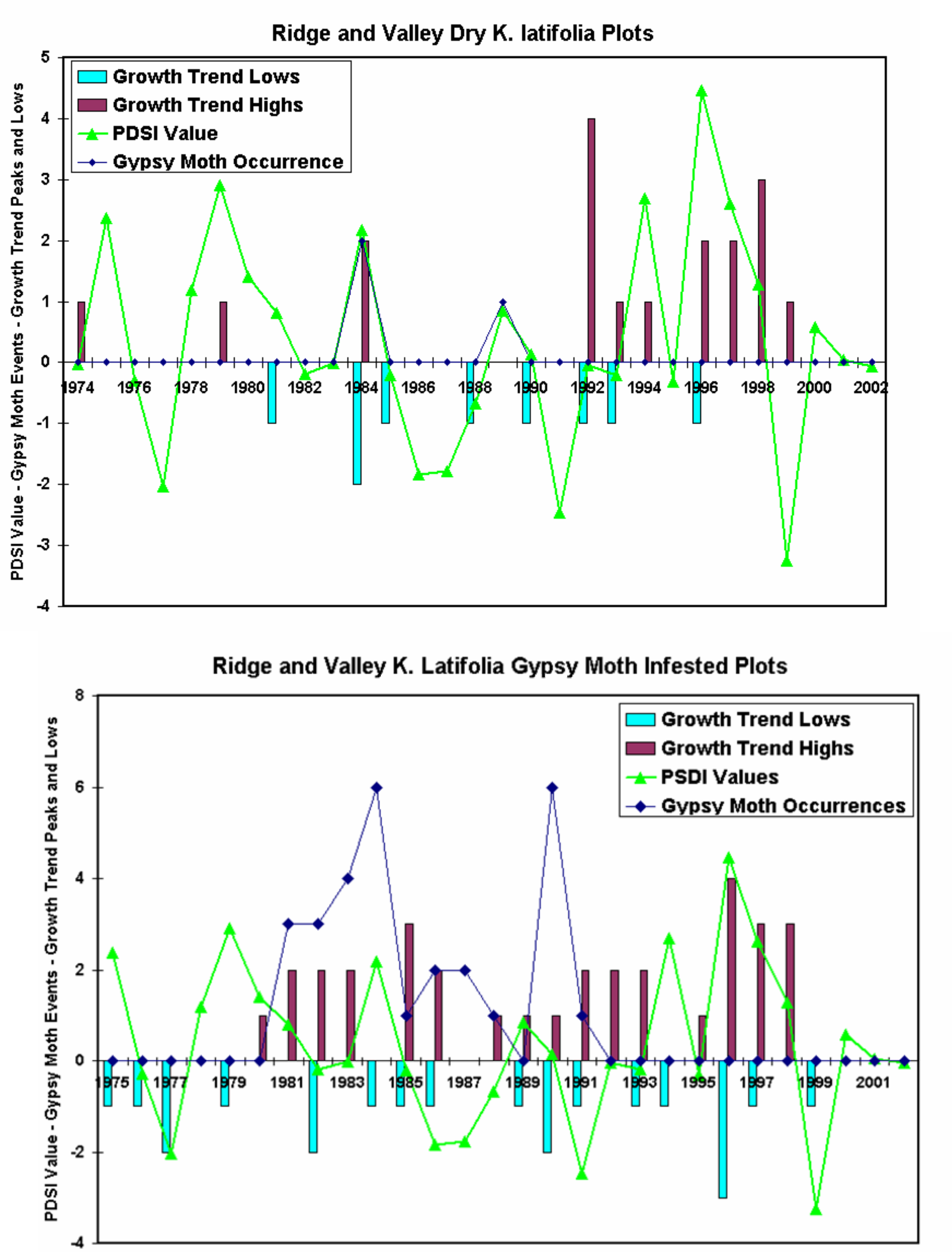


Figure 4.12. Peaks and lows identified in the generalized (4th order polynomial) trend lines of the growth ring data of the individual *K. latifolia* harvested in the Ridge and Valley study area. Peaks indicate a general release in the growth ring data. A preponderance of peaks occurred in the mid to late 1990s in the *K. latifolia* harvested from both the dry plots and those affected by gypsy moth infestations.

data originated. The low points in the biological growth curves did not converge in these ring series data. The same basic pattern for the timing of peaks in the biological growth curves was apparent in the *K. latifolia* harvested from gypsy moth infested plots.

In the *K. latifolia* individuals harvested from dry plots in the Allegheny Plateau, the pattern of growth curve peaks did not match the PDSI data temporally, except that the largest convergence of lows occurred during the dry year of 1991 (Figure 4.13). In the gypsy moth infested plots, a preponderance of peaks and lows occurred after the gypsy moth disturbance events of 1986 and 1987 as did a convergence of peaks after the defoliation wave of 1991.

In the *R. maximum* individuals harvested from dry plots in the Allegheny Plateau, the growth trend peaks converged in the wetter years of 1993 and 1996 through 1998 with lows occurring in the drought year of 1999 (Figure 4.14). In the gypsy moth disturbed plots, the highs occurred in a staggered manner during and after the 1991 infestations, with the lows again converging in dry 1999.

In the Ridge and Valley *K. latifolia* gypsy moth plots, a peak in the level of suppressions closely followed the timing of the onset of heavy infestation, and another peak in suppressions occurred just after the drought year of 1999 (Figure 4.15). Although a peak in releases occurred just before the onset of gypsy moth activity, it stabilized at a low level thereafter. The suppression and release patterns were not as striking in the *K. latifolia* plots that did not experience heavy gypsy moth activity, but a peak in

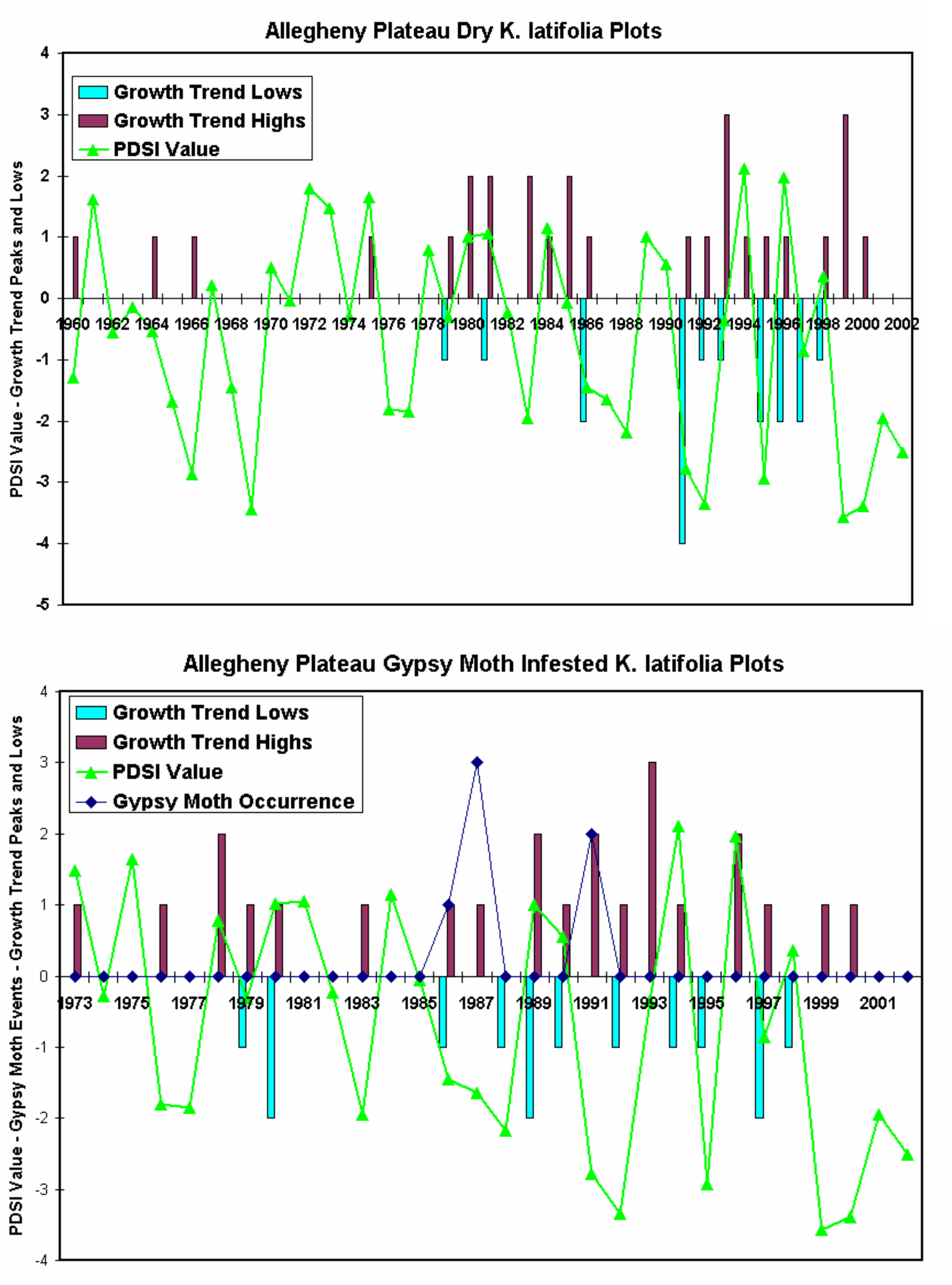


Figure 4.13. Peaks and lows identified in the generalized (4th order polynomial) trend lines of the growth ring data of the individual *K. latifolia* harvested in the Allegheny Plateau study area. Peaks predominate in the mid to late 1990s in the *K. latifolia* harvested from both the dry plots and those affected by gypsy moth infestations, but the gypsy moth plots show the prevalence of both peaks and lows associated with the general time of infestation.

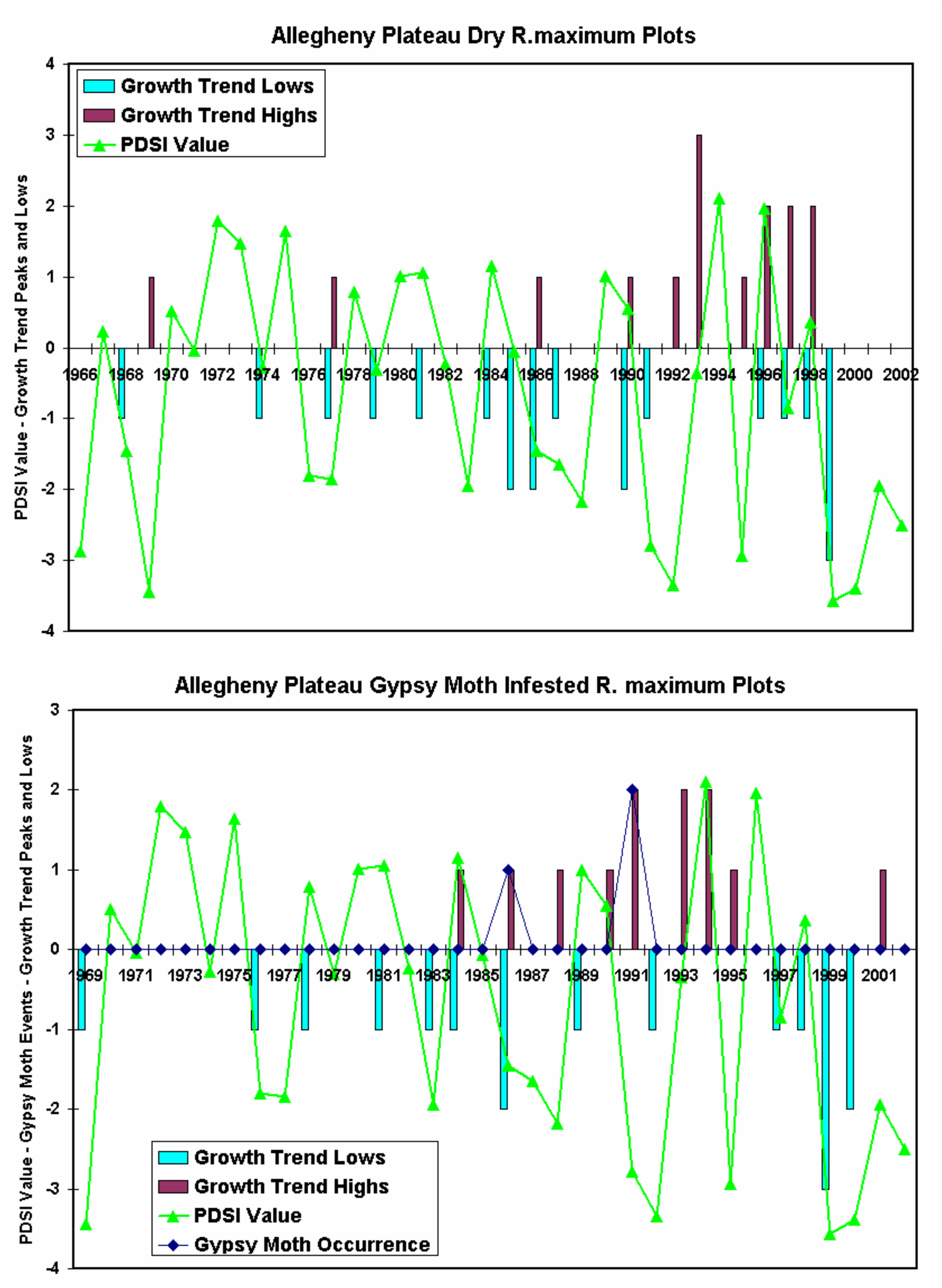
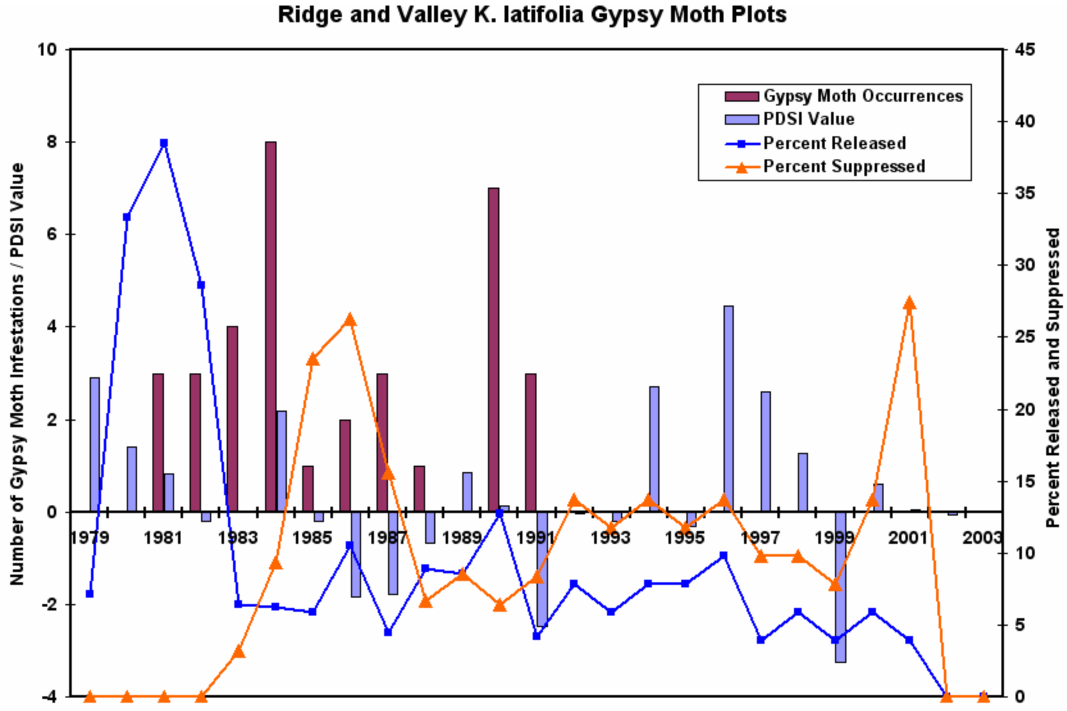


Figure 4.14. Peaks and lows identified in the generalized (4th order polynomial) trend lines of the growth ring data of the individual *R. maximum* harvested in the Allegheny Plateau study area. Peaks in the dry plots are more common in the wetter years of the mid to late 1990s, with lows most common during the extreme drought year of 1999. The predominance of peaks in the gypsy moth-affected plots coincide with the period just after infestation, with a prevalence of lows during the dry years of 1999 and 2000.



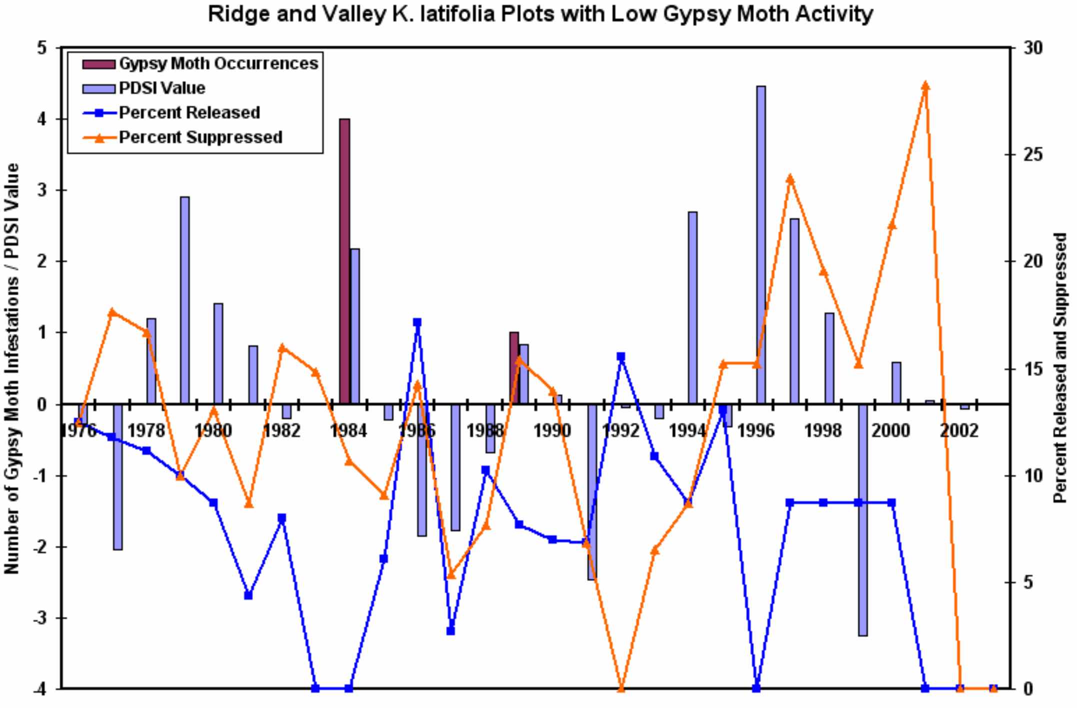


Figure 4.15: Percent of *K. latifolia* individuals that experienced growth suppressions and releases in the Ridge and Valley study area shown against the occurrence of gypsy moth infestations and timing of drought years as represented by Palmer drought severity index (PDSI) values averaged over the growing season months of May through September.

suppressions between 1997 and 2001 has some temporal correspondence with climatic fluctuations during that period.

In the Ridge and Valley dry *K. latifolia* plots, an unexplained peak in suppressions occurred in 1997, followed by a larger convergence in suppressions (40 percent suppressed) in 1999 that was likely related to the 1999 drought. Releases in these growth ring series data do not show a conspicuous pattern of temporal convergence. Although there is a general lack of conspicuous peaks among the suppressions and releases in the Ridge and Valley wet plot *K. latifolia* individuals, a peak in suppressions (23 percent) does occur between 1982 and 1984 (Figure 4.16). This may have resulted from the severe cold spell (-18˚ F) that occurred during the winter of 1982, perhaps causing greater leaf damage in downslope wetter areas due to cold air drainage.

The Ridge and Valley *R. maximum* plots that experienced gypsy moth defoliation did not exhibit a clear temporal pattern of growth jolts except for a spike in suppressions between 1962 and 1966, and this may be attributable to the period of consecutive drought years (Figure 4.17).

In the Allegheny Plateau *K. latifolia* plots that experienced gypsy moth disturbance, a peak in the amount of releases closely followed the first surge of defoliation in 1986-1987, and then peaked slightly again with the 1991 defoliation (Figure 4.18). Suppressions were not as prominent among the *K. latifolia* individuals on these plots. Releases in topographically dry and wet areas were timed in a rather haphazard fashion,

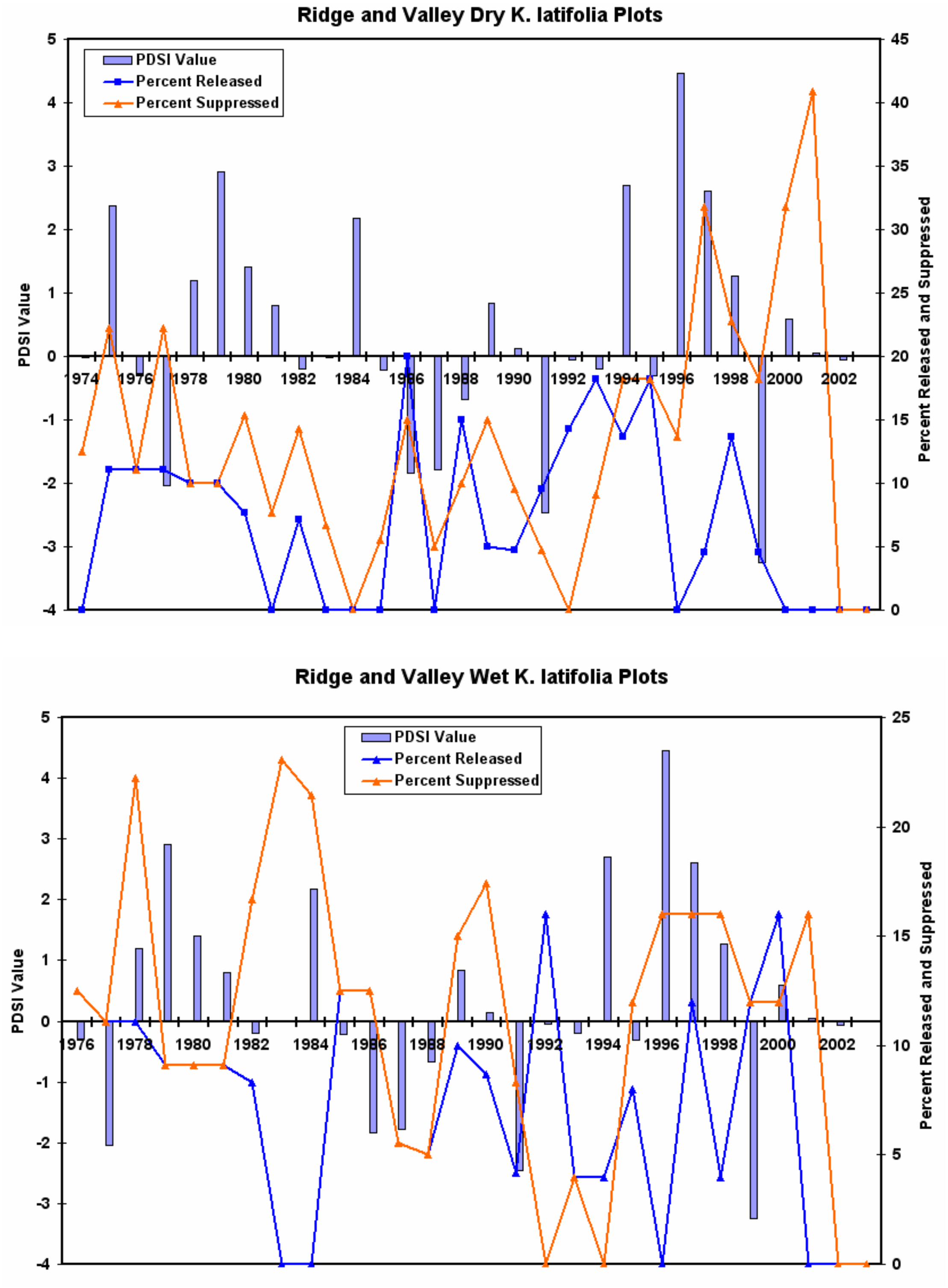


Figure 4.16: Percent of *K. latifolia* individuals that experienced growth suppressions and releases in dry and wet plots in the Ridge and Valley study area shown against the timing of drought years as represented by Palmer drought severity index (PDSI) values averaged over the growing season months of May through September.

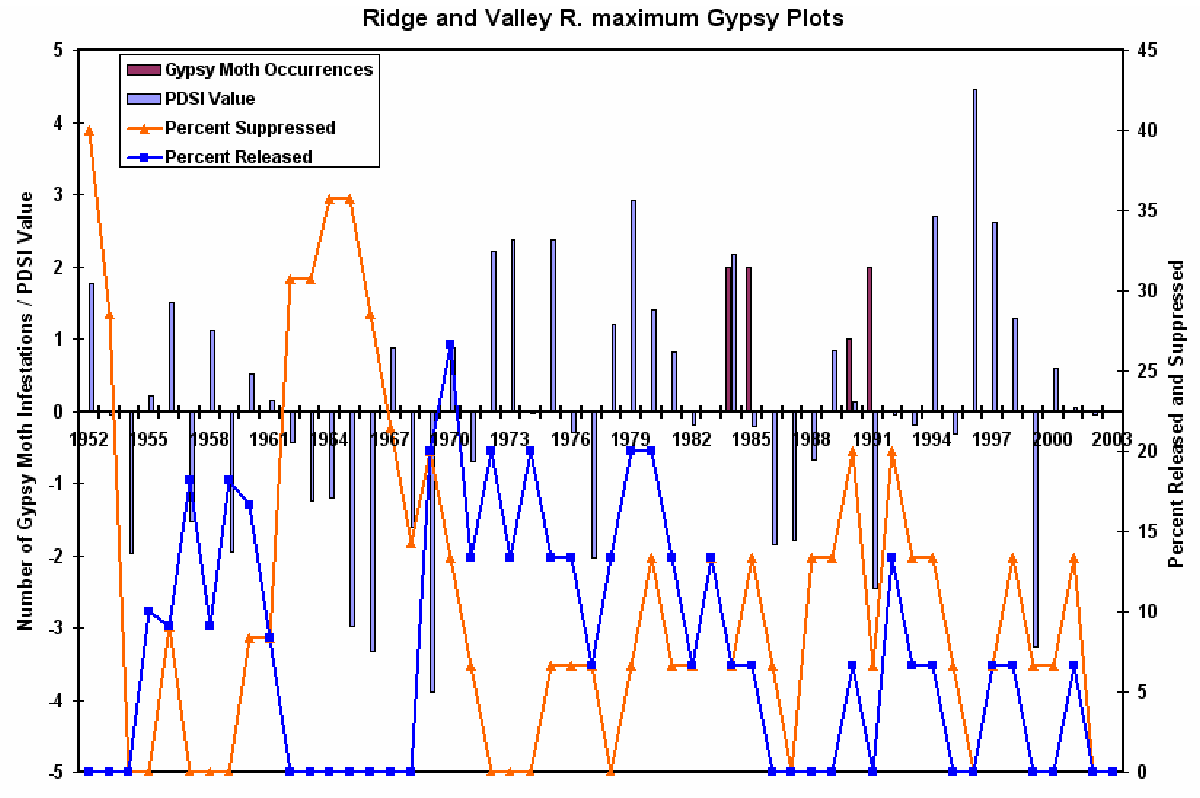


Figure 4.17: Percent of *R. maximum* individuals that experienced growth suppressions and releases in the Ridge and Valley study area shown against the occurrence of gypsy moth infestations and timing of drought years as represented by Palmer drought severity index (PDSI) values averaged over the growing season months of May through September.

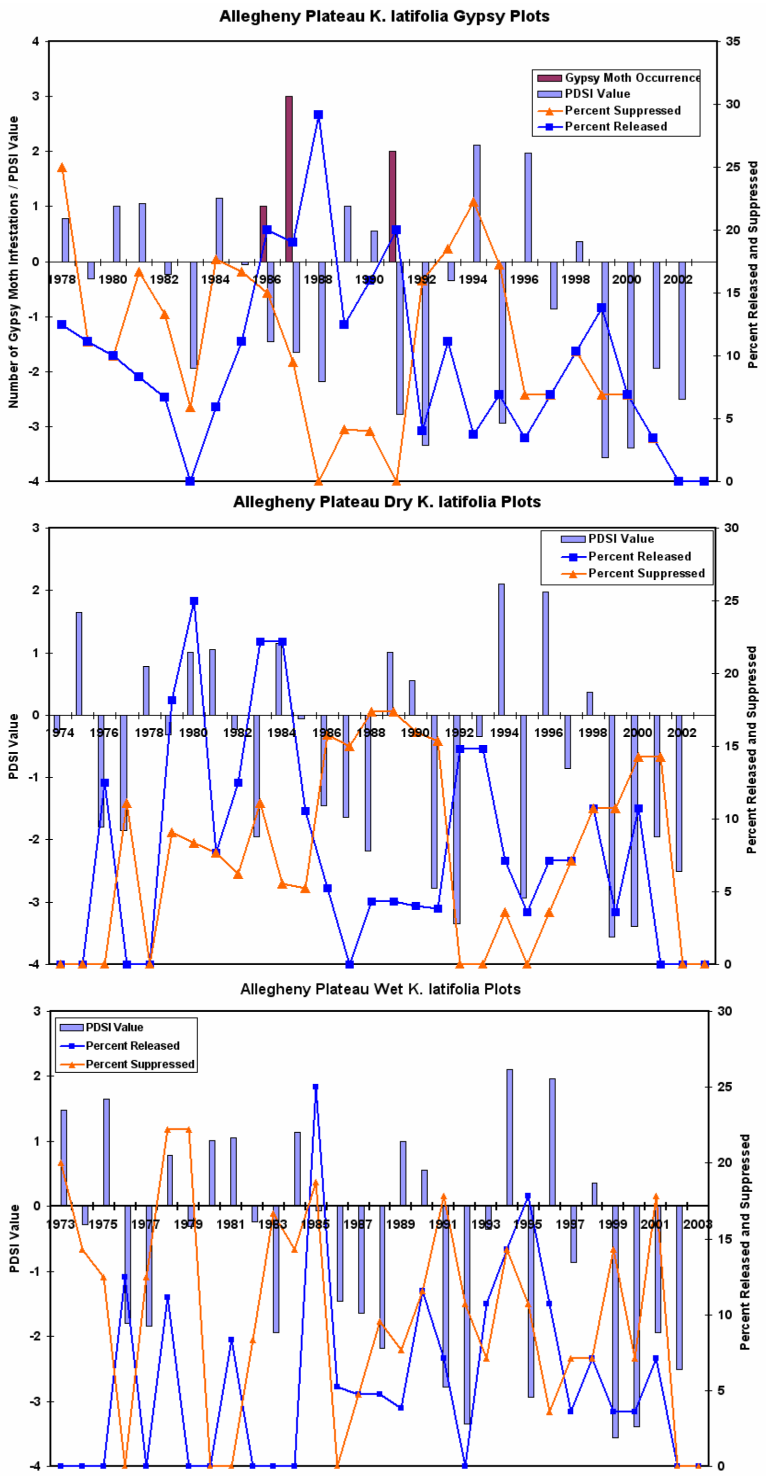


Figure 4.18: Percent of *K. latifolia* individuals that experienced growth suppressions and releases in the Ridge and Valley study area shown against the occurrence of gypsy moth infestations and timing of drought years as represented by Palmer drought severity index (PDSI) values averaged over the growing season months of May through September.

but generally were in keeping with the timing of non-drought years. Taken together with the remote sensing results, it appears that *K. latifolia* is not a particularly drought sensitive species, but rather a drought selected species that can thrive under extreme environmental conditions.

The timing of growth releases and suppressions in the Allegheny Plateau *R. maximum* growth ring series collected from gypsy moth infested plots show that suppressions outweigh releases in the years after the 1991 infestation (Figure 4.19). This suggests that changes in the canopy that may have occurred produced conditions that were more unfavorable for the growth of *R. maximum*, or conversely a number of additional *R. maximum* stems may have become initiated at this time, thereby increasing intraspecific competition. The latter explanation agrees with the observation from the remote sensing analysis that a net greening up occurred between 1991 and 1997 in defoliated Allegheny Plateau *R. maximum* areas (Figure 4.8). The *R. maximum* growth series data from both the dry and wet plots show a prevalence of releases over suppressions (except for a peak in suppressions in 1999 in the dry plots), indicating that growth conditions were generally favorable during the period after 1981.

4.4.3 Integration of Landscape and Plot-Level Analyses

The plot level observations (tree rings) and remote sensing data were examined separately for the most part, however a significant practical application of analyzing these data sets together lies in the potential to predict annual growth from remote sensing. In general, the relationships between growth increment and greenness are not expected to be

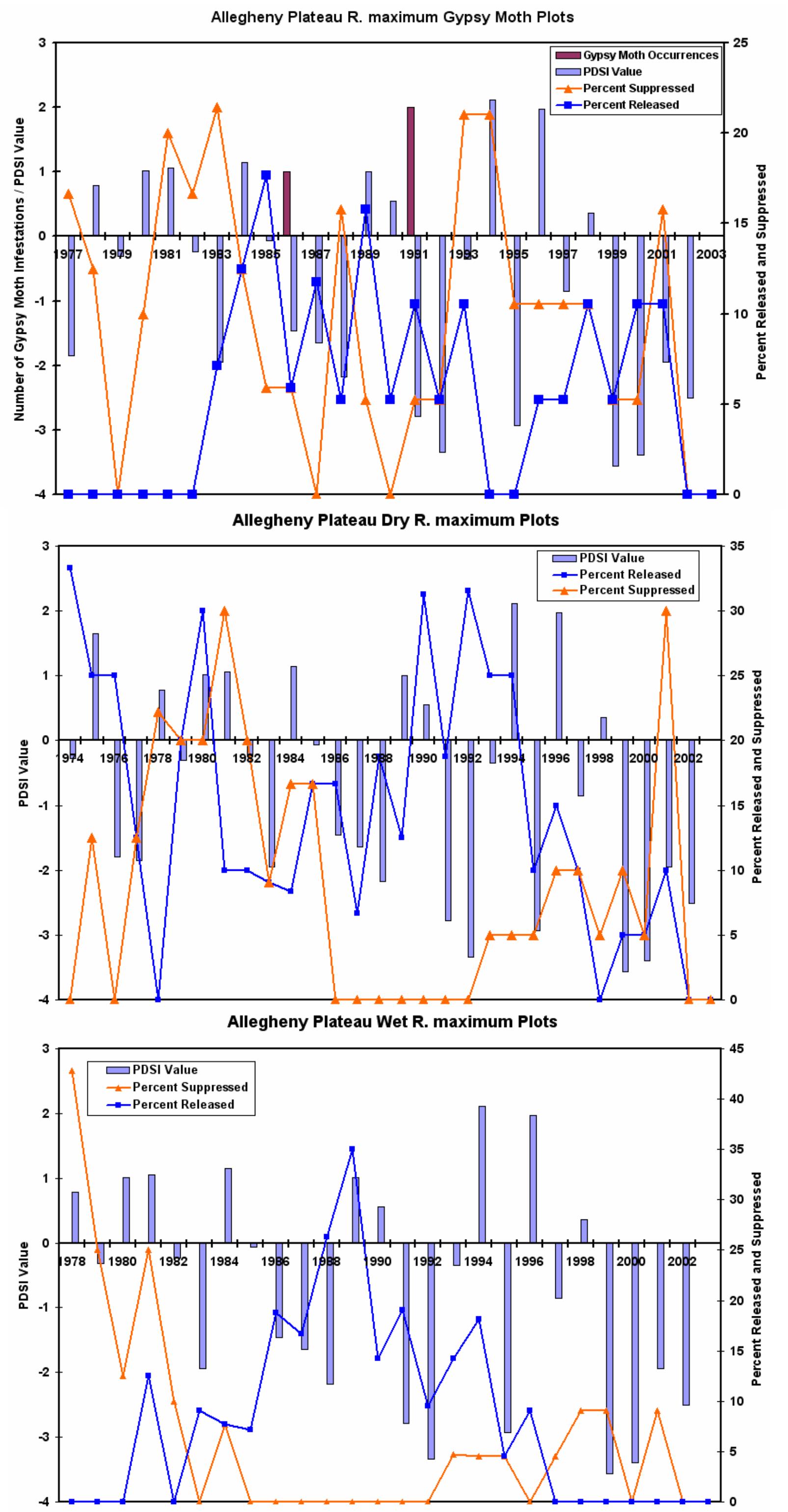


Figure 4.19: Percent of *R. maximum* individuals that experienced growth suppressions and releases in the Ridge and Valley study area shown against the occurrence of gypsy moth infestations and timing of drought years as represented by Palmer drought severity index (PDSI) values averaged over the growing season months of May through Sept.

strong because of high variability in growth among individual evergreen understory plot relationships. As such, patterns of 1999 growth increments of *K. latifolia* on Ridge shrubs on each plot. Because individual growth increments must be averaged to get a composite value per plot, intra-plot variability is expected to limit the strength of inter- and Valley plots were only weakly predicted by tasseled cap greenness in 2000 ($R^2 = .327$, $p = 0.021$), but this relationship was improved when the interacting factors stem density ($R^2 = .504$, $p = 0.01$) and stem density along with topography (TRMI) and gypsy moth disturbance history were considered ($R^2 = .563$, $p = 0.043$). In the Allegheny Plateau, the 1999 growth increments were only very weakly predicted on the mixed evergreen understory plots using tasseled cap greenness ($R^2 = .237$, $p = 0.108$) and the second principal component of all 6 of the Landsat TM bands ($R^2 = .262$, $p = 0.089$), but prediction using the latter remote sensing variable was moderately aided by the inclusion of topography (TRMI) into the regression ($R^2 = .403$, $p = 0.098$). On the Plateau *K. latifolia* plots, greenness was also a weak predictor of the 1999 growth increment ($R^2 = .27$, $p = 0.069$), but again the inclusion of TRMI improved the predictive power of greenness ($R^2 = .4$, $p = 0.078$). This analysis represents a promising research direction for direct integration of remote sensing and dendrochronological data, but greater controls on intra-plot variability may be needed to fully extend this application.

4.5 Discussion

By combining direct and indirect methods in a unique approach to change detection in this study, a more comprehensive assessment of the dynamic nature of the growth vigor of evergreen understory communities in the central Appalachian highlands has been gained than if only dendrochronology or remote sensing methods had been pursued. Although landscape scale spatial patterns of changes over time in the growth vigor of these communities can be tracked using remote sensing, the mechanisms behind these changes can only be investigated using ancillary data and field measurements. A combination of dendrochronology and remote sensing change detection identified connections between the timing of climatic fluctuation and gypsy moth disturbance and temporal patterns in growth vigor, and also illuminated the sometimes unexpected responses of *R. maximum* and *K. latifolia* to these perturbations. Moreover, the dendrochronology results provided validation of the remote sensing results.

On the landscape scale and local (microsite) scale, evidence of growth vigor changes corresponded temporally to the two broad-scale perturbations examined in this research. However, smaller perturbations that acted on the scale of the individual also occurred in the evergreen understory communities in both study areas, thus confirming the hypotheses posed for the dendrochronology portion of this research and providing partial explanation of the patterns of change detected in the remote sensing results. For example, the browning down of the *K. latifolia*, *R. maximum*, and 'mixed' evergreen understory communities observed in the remote sensing data between 1984 and 1986 in the Allegheny Plateau province was not substantiated in the annual growth ring series collected for either species. There was neither a convergence of lows apparent in the biological growth trends nor a peak in ephemeral growth suppressions apparent in these data. This suggested that the drop in growth vigor apparent in the remote sensing data was in error, and merely an artifact of phenological differences caused by the earlier acquisition time (March 24) of the 1986 image data. On the other hand, the drop in growth vigor apparent in the remote sensing data between 1997 and 2000 in both study areas is corroborated by the growth increment data in that an increase in the number of suppressions occurred in almost all of the categories of the growth ring series coinciding with the drought year of 1999 (as well as 2000 in the Plateau).

The hypothesis that evergreen understory communities dominated by *K. latifolia* and *R. maximum* are persistent on the landscape scale, but variable over time was also confirmed in the course of this research. On the landscape scale, both the *K. latifolia* and *R. maximum* communities in the Ridge and Valley province experienced a larger degree of greening up between 1984 and 2000 compared to the evergreen understory communities in the Allegheny Plateau province. The 'mixed' communities in the Plateau actually experienced a net browning down, except in the wetter areas. It was apparent that gypsy moth activity had an overall negative effect on the growth vigor of *K. latifolia* in the Ridge and Valley province between 1984 and 2000, but short-term gains in greenness were seen directly after the infestation. In the Allegheny Plateau, the *R. maximum* regions that experienced gypsy moth infestation showed a net greening up between 1984 and 2000. Topographically mediated drought severity proved to be an important correlate to growth vigor in the Allegheny Plateau study area, with *K. latifolia*, *R. maximum*, and 'mixed' communities all greening up to a significantly greater degree in wetter regions than in drier ones.

Tree ring data indicate that on the scale of the individual, changes in growth vigor over time – especially in response to perturbations – are complicated when examined on the yearly interval. Although the dendrochronological results from this research were helpful in closing the temporal gaps left by the four to five ‘snapshots’ provided by the remote sensing data and yielded insight into the mechanisms underlying changes that occurred, these results also pose a number of interesting research questions. Although *K. latifolia* appears to be quite drought tolerant, what mechanisms lie behind the counterintuitive result wherein suppressions increased in the Ridge and Valley *K. latifolia* during times of sufficient moisture availability and lack of gypsy moth activity? Is this a result of increasing inter- or intraspecific competition? Is the inherent increase in the amount of the ubiquitous fungal leaf spot (*Phyllosticta kalmicola*) or leaf blight (*Phomopsis kalmiae*) during wetter periods responsible for attenuation in overall growth vigor (Douglas 2003)? The responses of *K. latifolia* and *R. maximum* individuals to the two types of perturbation examined in this research also led to a number of questions. Do *K. latifolia* individuals respond to insect defoliation by growing fewer leaves or less wood, or are numerous new individuals initiated immediately following such a canopy disturbance, hence increasing intraspecific competition? Does *K. latifolia* respond to such an event by allocating more resources to root development or production of new ramets through layering? Finally, other factors may influence the temporal patterns of growth vigor. For example, how does a severe winter affect the growth vigor of *K. latifolia* and *R. maximum*? More substantial environmental data collection as well as tree ring data from canopy trees at these locations may provide further insight into the answers to these questions.

The appropriate design of an experiment to examine how *K. latifolia* - or *R. maximum* -dominated evergreen understory communities respond to gypsy moth defoliation requires the complete census all of the shrubs occurring within an area (preferably twice the size of the minimum mapping unit of a remote sensing platform if that component is to be implemented) so that the complete demographic structure of the area can be tied to events such as drought and/or canopy defoliation events. Knowledge of the timing of increases in *K. latifolia* and/or *R. maximum* stem density would help solve the conundrum concerning the relationship between growth releases and suppressions and the timing of gypsy moth infestation and climatic fluctuations. Cores from the canopy trees (live and dead) would also be valuable to so that a more complete reconstruction of the disturbance history of the canopy layer could be obtained.

Nevertheless, tree ring and remote sensing data exhibited distinct responses of *K. latifolia* and *R. maximum* to regional disturbance and climatic factors. Moreover, topographic position within physiographic provinces significantly influenced evergreen understory response to exogenous factors. Methodologically, both tree rings and remote sensing data were essential to the analyses. Although remote sensing data results did exhibit sensitivities to image timing, the results were more readily interpretable because they were less sensitive to microsite variations than the dendrochronology data.

Chapter 5: Carbon Sequestration and Nutrient Cycling Implications of the Evergreen Understory Layer

Abstract

Evergreen understory communities dominated by mountain laurel (*Kalmia latifolia* L.) and/or rosebay rhododendron (*Rhododendron maximum* L.) are an important but often overlooked component of Appalachian forests. Their carbon sequestration potential and nutrient storage and cycling impacts are among the principal ecological roles of these species. In this research, the carbon sequestration potential of evergreen understory species *K. latifolia* and *R. maximum* were defined through allometric modeling of their aboveground biomass along with other component forest species present at the scale of the watershed. The carbon sequestration and nitrogen and phosphorus storage potentials of these two species were investigated by running a 50-year simulation on forests comprising the canopy layer alone, then the canopy combined with the evergreen understory layer. When simulating forests in several test watersheds based only on the composition and biomass of the canopy layer, these forests have between 1631 and 4825 kg/ha less in overall carbon content and 41 to 224 kg/ha less nitrogen content than if the evergreen understory layer is included. Nitrogen uptake by evergreen understory vegetation was estimated to increase by between 6 and 11 kg N ha^{-1} yr^{-1} at year 50 for the canopy-with-understory forest compared to the canopy-only forest. Vegetation pool nutrient storage increased between 2 and 4 percent for nitrogen, and between 2 and 14 percent for phosphorus at year 50 when *R. maximum* and *K. latifolia* were included in the model. In addition, their aboveground standing biomass accounted for a only modest portion of the carbon sequestered and nitrogen stored by *R. maximum* and *K. latifolia* in the forest ecosystems studied at the watershed scale. Notable increases in the carbon and nitrogen amounts in the forest floor and soil pools were also found in forests modeled as a tree canopy-with-understory. Nitrogen storage predominated in the forest floor compared to the soil pool when a larger amount of *R. maximum* was present in a watershed, most likely due to the larger amounts of recalcitrant litter produced annually by this species compared to *K. latifolia*. In addition, storage of phosphorus in *K. latifolia* and *R. maximum* exceeded expectations compared to their watershed-scale standing biomass.

5.1 Introduction

The Appalachian highlands region contains some of the most extensive contiguous area of temperate forests in eastern North America. This has resulted in part from the infeasibility of transforming these areas into agricultural or urban land uses due to the high topographic relief (Robison 1960). These forests provide a number of societal services (Daily *et al*. 1997), among them the maintenance of air and water quality and nutrient storage through efficient internal cycling (Perry 1998, Aber *et al*. 2000). They are also important on a global scale as a carbon sink capable of attenuating climatic changes caused by increases in atmospheric carbon (Schlesinger 1977, Sedjo 1992, Currie *et al*. 2003). It has been suggested that forests that contain an evergreen component tend to be characterized by slower nutrient cycling compared to that found in purely deciduous stands (McGinty 1972, Thomas and Grigal 1976, Day and Monk 1977, White et al. 1988). As such, the amount and species composition of the evergreen vegetation component of a forest stand is relevant to the nutrient cycling and carbon sequestration capacity of eastern temperate forests in general, and in particular related to its capacity to improve air and water quality and act as a carbon sink to potentially mitigate climate change. In Appalachian highland forests, this evergreen component includes conifers and firs in the canopy stratum as well as the broadleaf evergreen species present in the understory stratum, which is often dominated by mountain laurel (*Kalmia latifolia* L.) and/or rosebay rhododendron (*Rhododendron maximum* L.).

The different species present in a forest have unique nutrient cycling capacities, originating from both their size and growth strategies. Canopy tree species are impotant in both short- and long-term nutrient cycles; nutrient rich ground layer species are notable in the annual cycle; and evergreen species are influential in cycles of intermediate length (Day and Monk 1977). Evidence suggests that some deciduous species such as red maple (*Acer rubrum*) tend to speed up the nutrient cycling of forest ecosystems, while evergreen species such as sclerophyllous shrubs and conifer species such as hemlock (*Tsuga* *canadensis*) tend to slow it down (W. Currie, pers. comm.). Specifically, the evergreen understory species *K. latifolia* and *R. maximum* are significant with respect to carbon storage and nutrient cycling in Appalachian forests, because they produce slowly decomposing leaf litter, thereby regulating seasonal nitrogen availability and influencing long-term patterns organic matter accretion in early to mid-successional Appalachian forests (White et al. 1988). The lignous nature of *K. latifolia* and *R. maximum* leaves causes them to decay on the forest floor at a much slower rate compared to deciduous leaves (Thomas and Grigal 1976). In fact, the ability of *K. latifolia* to inhabit dry, sterile sites has been linked to their tendency to slowly return nutrients to the soil and create extremely tight mineral cycles through the gradual leaching of nutrients from leaves that fall year-round and become slowly decaying litter (Monk 1966, Thomas and Grigal 1976).

Evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* have been estimated to cover three million acres of forested land in the Southern Appalachian Mountains (Wahlenburg and Doolittle 1950), while *R. maximum* is said to be the dominant subcanopy species in an estimated 74 million acres in that region (Rivers *et al*. 1999). Moreover, *R. maximum* and *K. latifolia* appear to have steadily increased in importance in the forests of the southern and central Appalachian Mountains over the 20th century due to canopy tree disease, management practices, and other disturbances (Smith 1963, Romancier 1970, Monk *et al*. 1985, Phillips and Murdy 1985, McGraw 1989, Baker 1994, Dobbs 1995). In this context, the *K. latifolia*- and/or *R. maximum*-dominated evergreen understory layer may represent a significant component of the standing biomass of central Appalachian forests that heretofore has not been quantified. The objective of this study is to quantify the prevalence, ecological impacts, and potential future influence of these evergreen understory shrub species on aboveground biomass, carbon sequestration potential, and nitrogen and phosphorus storage in central Appalachian forests.

In this study, the spatial extent of the *K. latifolia*- and/or *R. maximum*-dominated evergreen layer was evaluated using Landsat Enhanced Thematic Mapper (ETM) imagery and ancillary information in two study areas in the central Appalachian highlands; one located in the warm and dry Ridge and Valley province and another located in the cool and wet Allegheny Plateau province. Field data were used in conjunction with spatial data to estimate standing crop and growth parameters of these species, with the ultimate objective of determining their carbon sequestration potential and nitrogen cycling on a landscape scale. Mapping of the evergreen understory layer was undertaken because no good maps of evergreen understory distribution currently exist for this region. For example, the national land cover data set (NLCD), produced by the multi-resolution land characteristics (MRLC) consortium (Vogelmann *et al*. 2001) used Landsat Thematic Mapper (TM) image data to map land cover classes on a regional scale, but only identified three forested classes – deciduous, evergreen, and mixed, with no distinctions made to identify the broadleaf evergreen understory component of otherwise broadleaf deciduous forests (usually mapped as mixed conifer or evergreen, both incorrect).

5.2 Research Objectives

The objective of this research is to quantify the aboveground biomass and capacity to store carbon and nutrients of *R. maximum* and *K. latifolia* in the Ridge and Valley and Allegheny Plateau of the central Appalachian highlands (Figure 5.1). Standing biomass is estimated using plot-level observations extrapolated to the watershed scale via satellite remote sensing. In addition, the carbon sequestration and nitrogen and phosphorus storage potential of the overall forest and the evergreen understory layer species *R. maximum* and *K. latifolia* are calculated using a nutrient cycling spreadsheet (NuCSS) model (Verburg and Johnson 2001) to determine their importance as components of these forest ecosystems.

Evergreen understory communities tend to be extensive locally, but may also be absent across broad areas. In this study, the importance of these species was examined specifically within several test watersheds where their coverage was extensive, although overall values will be derived for the entire area as well. The research was organized to:

1) Estimate total aboveground biomass and leaf biomass of *K. latifolia* and *R. maximum* in the study areas,

2) Relate these values to the overall biomass of the forests growing in seven watersheds within the Allegheny Plateau and Ridge and Valley provinces,

3) Use the forest canopy and evergreen understory layer biomass estimates to simulate the carbon sequestration and nitrogen and phosphorus accumulation potentials of forests within these watersheds,

4) Simulate carbon and nitrogen storage dynamics over time in these watersheds, and

5) Calculate the differences between simulating these forests as comprising only the canopy layer and simulating them as a canopy layer combined with an evergreen understory.

A key goal of the work is to evaluate the importance of evergreen shrubs in forest ecosystem functioning, and to illustrate issues that arise when considering only the forest canopy layer when modeling carbon and nutrient storage.

5.3 Methods

5.3.1 Study Area

Biomass and nutrient cycling implications of the evergreen understory shrubs *R. Maximum* and *K. latifolia* were examined in two representative study areas of the central Appalachian highlands (Figure 5.1). Nineteen vegetation plots were sampled in the warm and dry Ridge and Valley physiographic province (Green Ridge State Forest, GRSF, and Buchanan State Forest, BSF). The Ridge and Valley sites are located within the oak-chestnut forest type (Braun 1950) and were heavily logged and extensively burned between 1879-1910 (Mash 1996), but now are largely mature 50-75 year old forests (unpublished data, MD and PA continuous forest inventories). The three watersheds used for simulation in this study are located in the BSF (Figure 5.2), which unlike GRSF was not planted in fruit orchards in the early 20th century and therefore does not have confounding land use history factors that might influence this study. Elevation ranges from 123 – 845 m with steep northeast-southwest trending ridges. The temperature

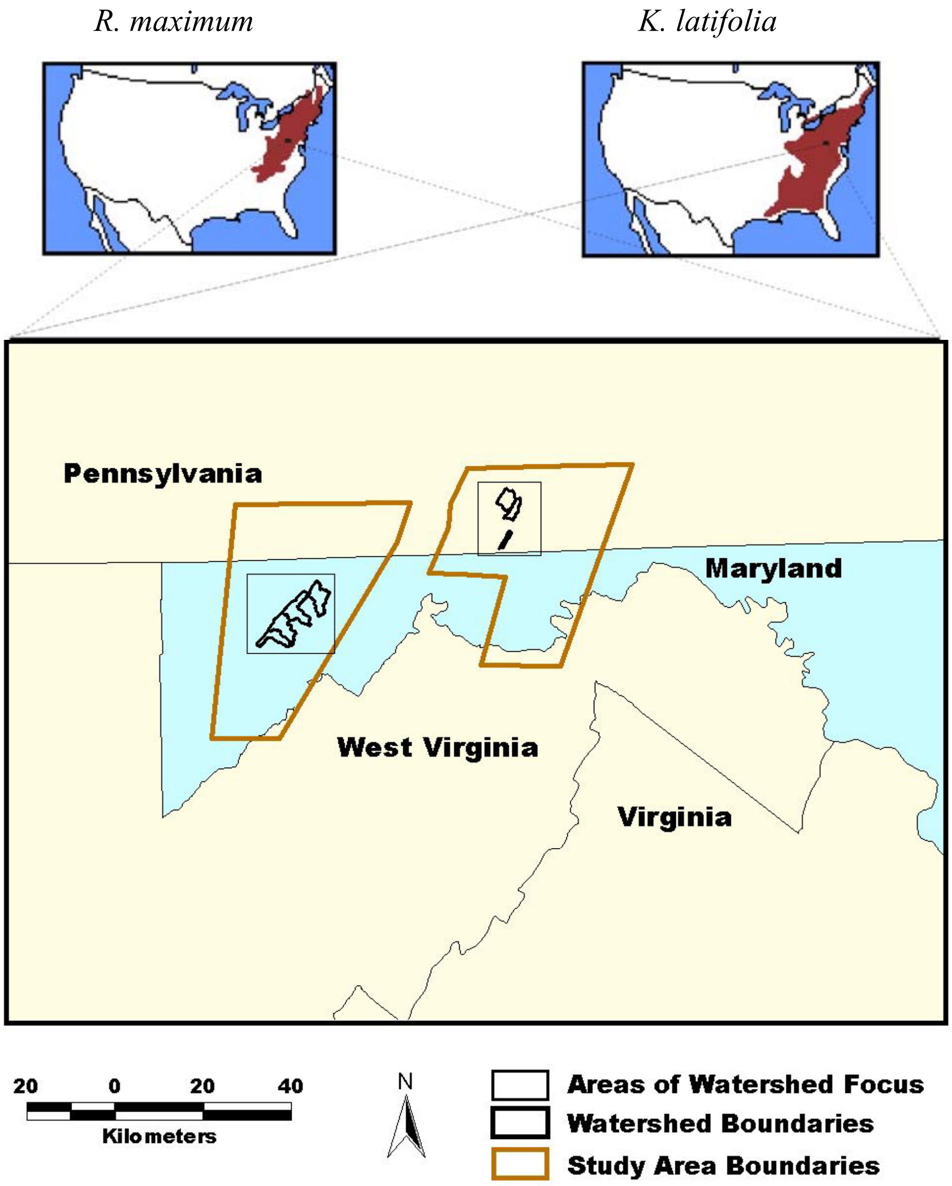


Figure 5.1: Geographic range of rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) and area map of present study showing the boundaries of the Allegheny Plateau and Ridge and Valley study areas as well the boundaries of seven watersheds chosen for intensive study. The watershed focus rectangles are the map extents in Figures 5.2 and 5.3.

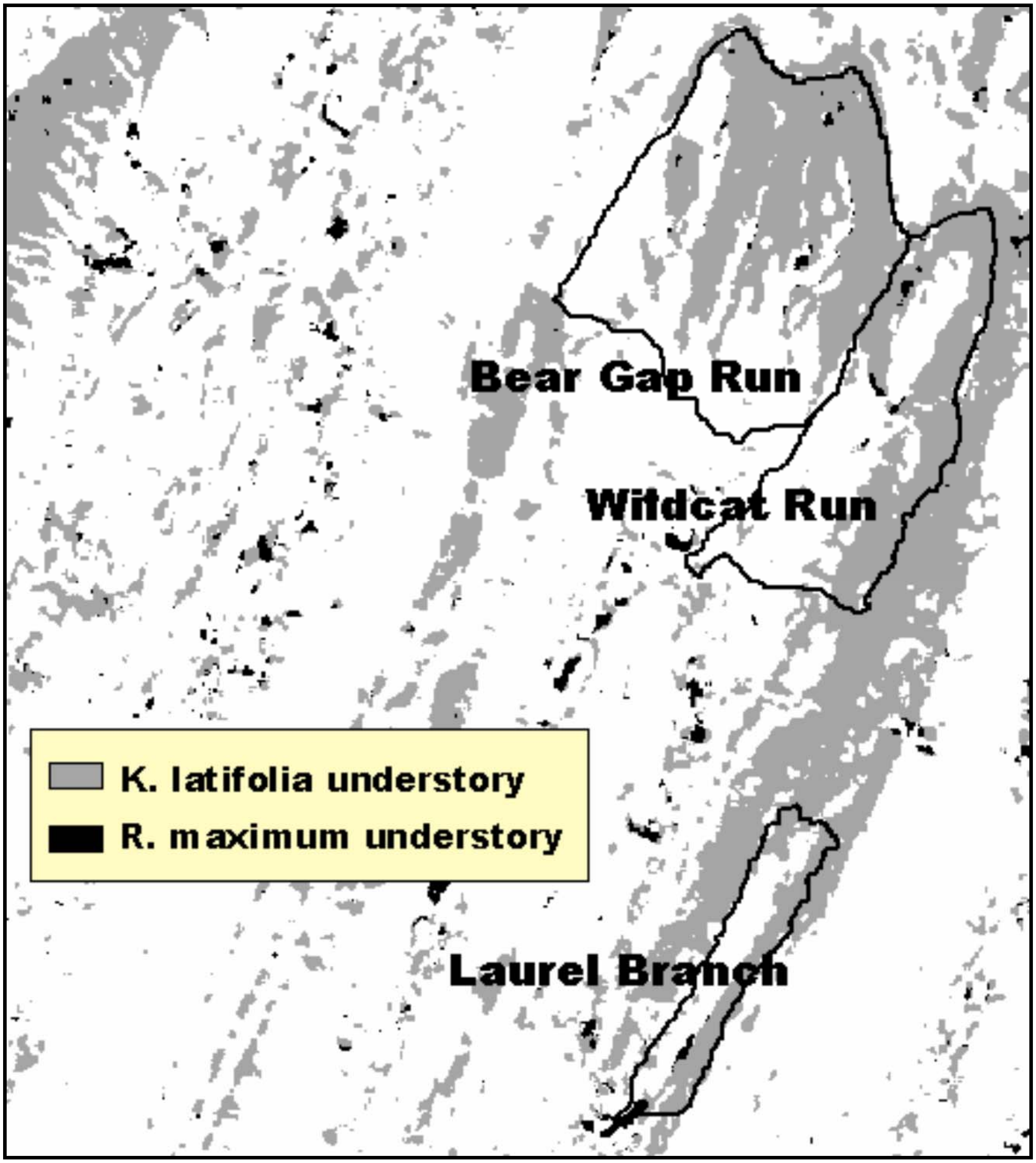


Figure 5.2. Map of three test watersheds examined in the Ridge and Valley study area.

ranges from 2.3 – 15.8 deg C annually (Stone and Matthews 1974), with an average annual precipitation of 1023 mm (Lynch, pers. comm.) and actual evapotranspiration (AET) of 537 mm/yr (NCDC 1948-1993, K. Eshelman, unpublished data). 27 field plots were located on the Allegheny Plateau (Savage River State Forest, SRSF, Figure 1.3) in the mixed mesophytic forest zone (Braun 1950). Like the ridge and valley these forests were largely cut in the early 20th century and are now dominated by oaks, but also have a substantial component of conifers, including hemlock (*Tsuga canadensis*) and numerous pine species (*Pinus spp*.). The watersheds used for simulation are located in typical narrow first-order tributaries of Savage River (Figure 5.3). Elevation ranges from 304-986, with temperatures ranging from -14 – 31.6 deg C annually (NCDC 1951-2002), with an average annual precipitation of 1216 mm (Lynch, pers. comm.), and AET of 587 mm/yr (K. Eshleman, unpublished data).

5.3.2 Watershed Delineation

Three first order watersheds were selected for intensive study in the Ridge and Valley (Figure 5.2) and four watersheds in the Allegheny Plateau study area (Figure 5.3). All seven watersheds exhibited a prevalence of evergreen understory communities dominated by *K. latifolia* and/or *R. maximum*. Overall standing biomass and leaf biomass were estimated within each watershed to characterize carbon content and nitrogen and phosphorus cycling. Watershed boundaries were delineated using automated tools in the Arc/Info GRID module on 7.5 minute (30 meter cell) USGS digital elevation models (DEM). A 30-meter map of evergreen understory communities derived from Landsat data was overlaid on the watershed data to determine the coverage of *K. latifolia* and/or *R. maximum* in the individual watersheds (Table 5.1).

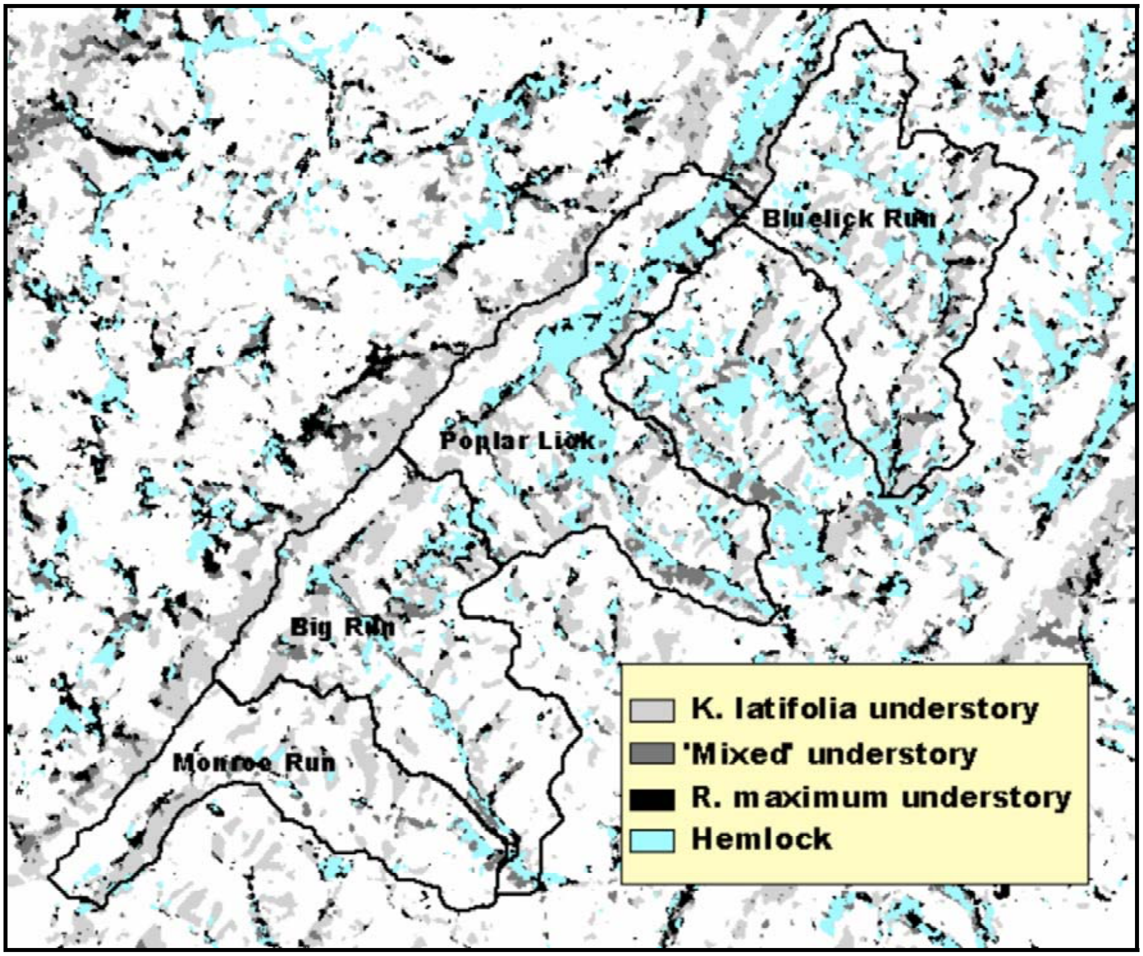


Figure 5.3. Map of four test watersheds examined in the Allegheny Plateau study area.

Table 5.1. Overall area, forested area, numbers of vegetation survey plots used to estimate biomass, and spatial extents of evergreen understory community types in each of the watersheds examined in this study. Note that the parenthetically indicated percentages of cover relate only to forested portions of these watersheds. Vegetation inventory data from Continuous Forest Inventory (1 plot from USFS Forest Inventory and Analysis (FIA)

Watershed	Area (ha)	Forested Area	Inventory Plots	Ha *K. latifolia* cover (%)	Ha *R. maximum* cover (%)	Ha 'Mixed' cover (%)
Ridge and Valley province						
Bear Gap Run	1325.1	1308.4	7	671.9 (51.4)	9 (0.7)	--
Laurel Branch	288.36	287.1	7	123.1 (42.9)	7.3 (2.5)	--
Wildcat Run	793.6	744.7	7	333.5 (44.8)	4.4 (0.6)	--
Allegheny Plateau province						
Big Run	1979.6	1859.6	35	399.4 (21.5)	119.5 (6.4)	104 (5.6)
Bluelick Run	1898.9	1554.8	15	402.3 (25.9)	171.8 (11)	88.4 (5.7)
Monroe Run	1376.2	1271.3	21	256.3 (20.2)	47.6 (3.74)	48.8 (3.8)
Poplar Lick	2115.9	1885.4	22	464.6 (24.6)	206.4 (10.9)	129.5 (6.9)

5.3.3 Forest Aboveground Biomass Estimates

Evergreen Understory Layer

The aboveground biomass for *R. maximum* and *K. latifolia* was estimated using regression equations relating stem density to biomass (Monk *et al*. 1985). Spatial representations of stem density (and hence biomass) were obtained by regressing the stem density (stems/ha) measured on field plots established for this research against the spatially corresponding value of the greenness component of a Tasseled Cap transformation of Landsat Enhanced Thematic Mapper (ETM) data acquired on March 31, 2000 (Figures 5.4 and 5.5). Because this image pre-dates leaf-out conditions, the image can be considered representative of evergreen (only) greenness. Observations were removed from the analysis that corresponded to field plots where understory hemlock and/or white pine or mixed conifer canopy were present. Because areas containing evergreen understory communities dominated by *K. latifolia* and/or *R. maximum* in both the Ridge and Valley and Allegheny Plateau study areas had previously been mapped to better than 80 percent accuracy level using Landsat image data (Chapter 3), these regressed stem densities were scaled up only for the areas mapped to each evergreen understory community type (*R. maximum*, *K. latifolia*, and mixed *R. maximum* and *K. latifolia*). It was assumed that the 'Mixed' evergreen understory areas in the Allegheny Plateau region contained an equal proportion of both *R. maximum* and *K. latifolia*. Because it was observed from field data in the Allegheny Plateau province that *R. maximum* or *K. latifolia* were present in many areas also containing hemlock (with some confusion between evergreen understory and hemlock-containing land cover

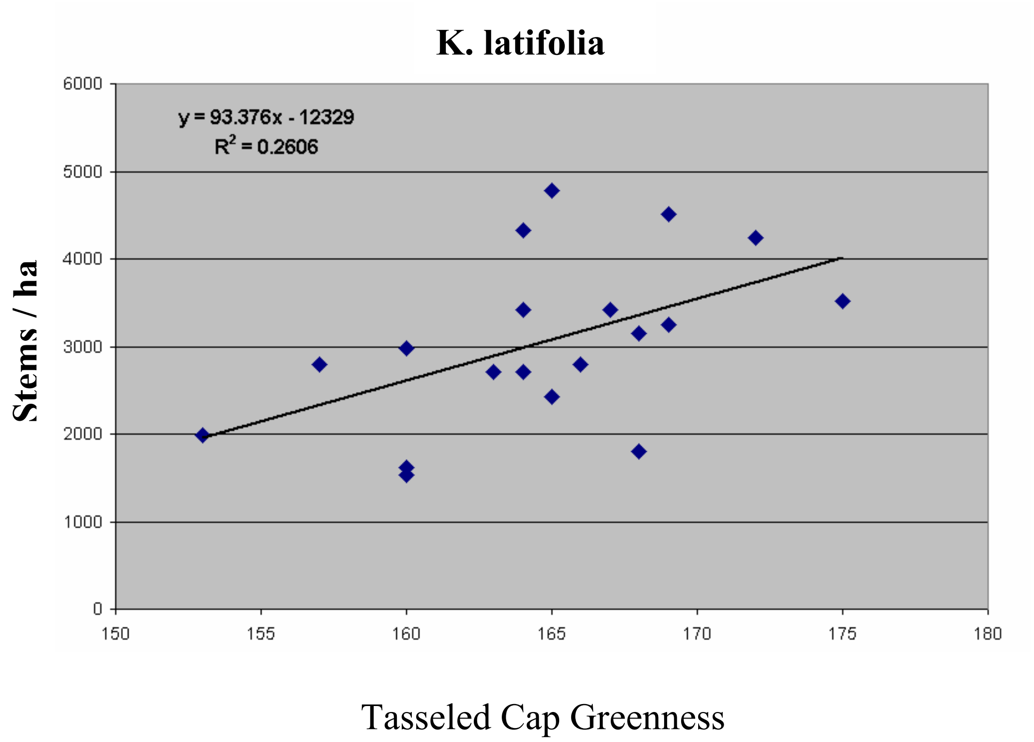


Figure 5.4. Regression from which biomass estimate was based for evergreen understory communities dominated by *K. latifolia* in the Ridge and Valley study area (df 1/17, F = 5.99, p = .026).

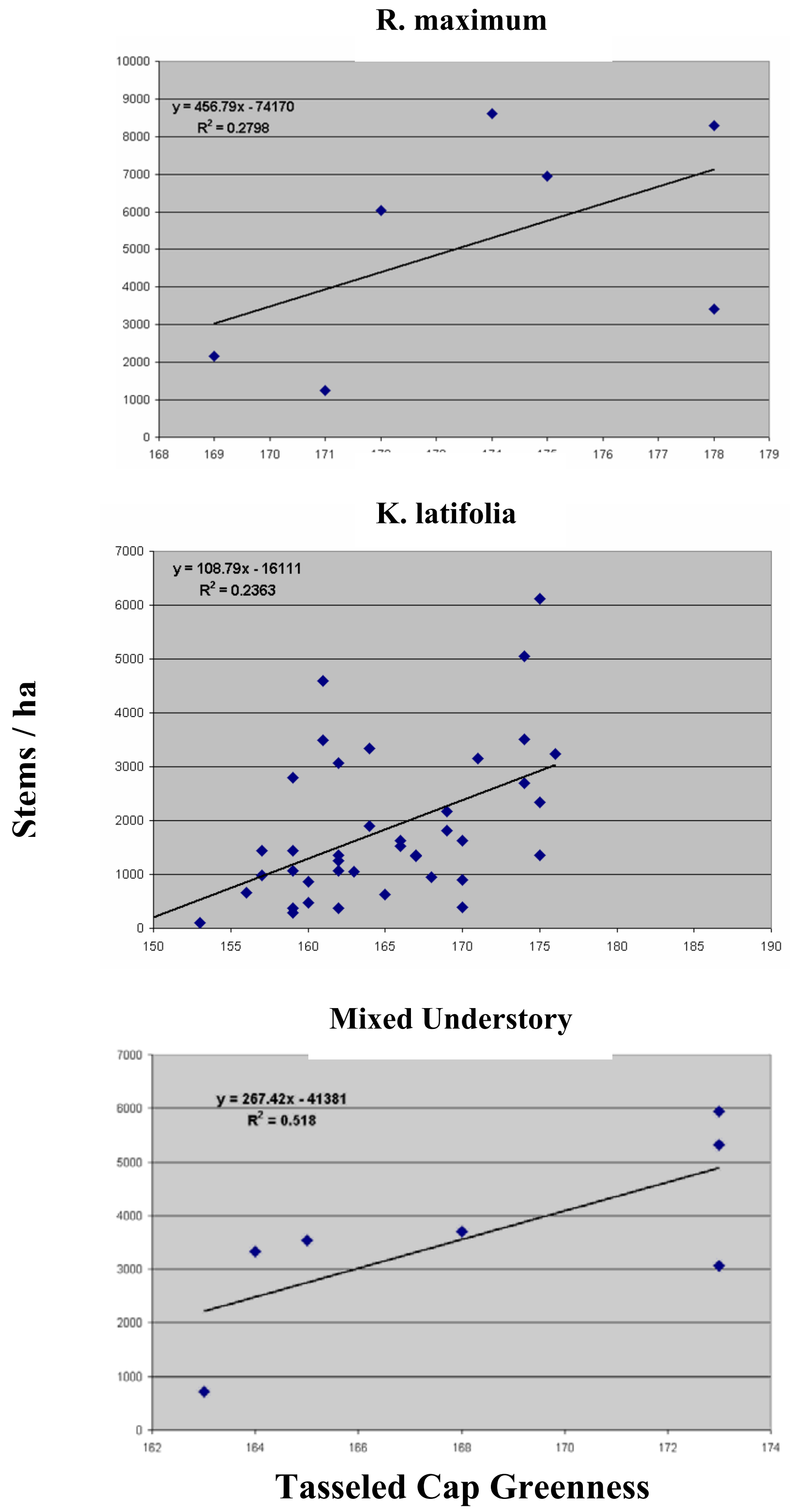


Figure 5.5. Regressions from which were based the biomass estimates for *K. latifolia*, *R. maximum*, and 'Mixed' understory areas in the Allegheny Plateau study area (*R. maximum* df 1/5, F = 2.27, p = .192; *K. latifolia* df 1/38, F = 12.21, p = .001; 'Mixed' df 1/5, F = 6.77, p = .048).

categories, Chapter 3), half of the pixels classified as containing hemlock were added to the estimates of evergreen understory stem density. Recognizing that all maps contain errors, this correction was made to prevent underestimation of evergreen understory, and was implemented by assuming that the weighted average stem density of each of *R. maximum* and *K. latifolia* were present in 25 percent of the hemlock-classified pixels.

Regression equations (Table A22) were applied to estimate biomass from the stem diameters of *R. maximum* and *K. latifolia* using average stem diameter values for each species established in Chapter 4. In that study, wood discs from 331 *R. maximum* and *K. latifolia* stems were strategically collected in areas representative of various drought stress conditions and gypsy moth disturbance levels from 19 vegetation plots in the Ridge and Valley and 27 plots in the Allegheny Plateau. The average stem diameter or *K. latifolia* was 3.0 cm in both study areas. The average stem diameter for *R. maximum* was 5.3 cm in the Ridge and Valley and 4.0 cm in the Allegheny Plateau. Using these stem diameters and the modeled stem density, values for the woody, foliar, and total aboveground biomass were estimated using equations developed by Monk *et al*. (1985) for both species on a per-hectare basis at the scales of the entire study area and selected watersheds (Tables 5.5 and 5.6).

Forest Canopy

The aboveground biomass of the forest canopy trees was estimated from plot-level field surveys of species composition and DBH using a series of allometric equations (Table A22) developed for tree species groups (Jenkins *et al.* 2003). These equations were applied to field data from 366 continuous forest inventory (CFI) plots in the Allegheny Plateau study area. Because the Ridge and Valley study area straddles two states, its forest canopy tree aboveground biomass was estimated using 463 CFI plots in Maryland and 5 forest inventory and analysis (FIA) plots located in Pennsylvania. A subset of the CFI plots were chosen to estimate the aboveground biomass within the four watersheds in the Allegheny Plateau based on GIS overlays (Table 5.1). In the Ridge and Valley, only 6 CFI plots and 1 FIA plot coincided with the area encompassing the three test watersheds and were in close spatial proximity to evergreen understory communities mapped using remote sensing (Chapter 3). In both study areas, allometric equations were used to estimate total aboveground biomass and the proportion of foliar material. The biomass estimates were applied to the CFI and FIA plots, then extrapolated to the study areas as a whole and test watersheds in particular based on the remote sensing classification.

5.3.4 Simulation of Carbon and Nitrogen Storage and Cycling

Nutrient Cycling Spreadsheet Model (NuCSS)

The nutrient cycling spreadsheet model (NuCSS, Verburg and Johnson 2001) model was applied to estimate carbon sequestration and to track nitrogen and phosphorus storage over time for the forests occurring within the seven test watersheds. NuCSS is a spreadsheet-based compartment model that tracks carbon and nutrient storage, fluxes, and cycling through standing biomass, the forest floor, and soil storage pools. It was designed to serve as a tool for nutrient management, and as such is intermediate in complexity between simple budget calculations and complex, process-based ecosystem models (Verburg and Johnson 2001). For example, there is no feedback between the soil nutrient availability and tree growth. Exchangeable soil cation and nitrogen pools will become negative if nutrient requirements of tree growth exceed what is available in these pools (Verburg and Johnson 2000). The primary utility of NuCSS for this work lies in comparison of results developed for forests consisting of canopy trees only with forests in which evergreen understory layer dominated by *K. latifolia* and/or *R. maximum* are properly characterized

The growth model within the NuCSS model allows the user to 'grow' a forest community over 50 1-year time steps using a logistic growth function for foliage, branch, bole, and coarse and fine root compartments. Initial and maximal biomass amounts are required inputs to initialize simulations. The equation used in the NuCSS model to 'grow' these vegetation compartments is:

$$W(t) = W_{max}/(1 + \acute{\alpha} e^{-\mu t})$$

where $W(t)$ is biomass at time t, W_{max} is the maximal biomass, $\acute{\alpha}$ is the parameter that describes the steepness of the exponential growth slope, μ is the relative growth rate, and t is time (Verburg and Johnson 2000). It is important to note that vegetation growth is not limited by the availability of soil nutrients, but is imposed on the simulation of nutrient cycling, with soil exchangeable cations and N becoming negative if growth nutrient requirements exceed availability.

Decompositon and mineralization of leaf, woody, fine root litter, and soil organic matter is calculated using an exponential decay function defined by decomposition rate constants (k-value) defined separately for leaf litter, wood, and fine roots. At each time step (t), the amount of organic matter present is computed as:

$$OM(t) = OM(t-1) - OM(t-1) * K$$

Where OM(t) is the amount of organic matter present at time t and K is the decomposition rate constant.

The N cycle is simulated in NuCSS by allowing N to enter the litter pool from live foliage, branches and fine roots is computed using the equation (foliar litter used for this example):

$$N_{litter} = N_{foliage} * (f_{f->1} * (1 - f_{transl}))$$

Where $N_{foliage}$ is the amount of N in the live foliage, $f_{f->1}$ is the fraction of live foliage biomass entering the litter pool, and f_{transl} is the fraction of N translocated before leaf senescence (Figure 5.6). These parameters are set by the model user. It is assumed that N inputs to the litter pool from foliar leaching are indistinguishable from N originating from litterfall, so both are included in N_{litter} (Verburg and Johnson 2000). The N in the litter pool is either mineralized or immobilized by microorganisms, depending on the C/N ratio of the substrate, the fraction of C in the litter (F_c), microbial C/N (C/N_{mic}), and microbial carbon use efficiency (CUE_{mic}). The N present in the OM that exceeds what is necessary for microbial biomass production is mineralized, and the rest is immobilized. Mineralization and immobilization of N is calculated using the equation:

$$N_{miner/immob} = F_C * OM(t-1) * K/(F_C * OM(t-1)/N-t-1)) - CUE_{mic} * F_C * OM(t-1) * K/(C/N_{mic})$$

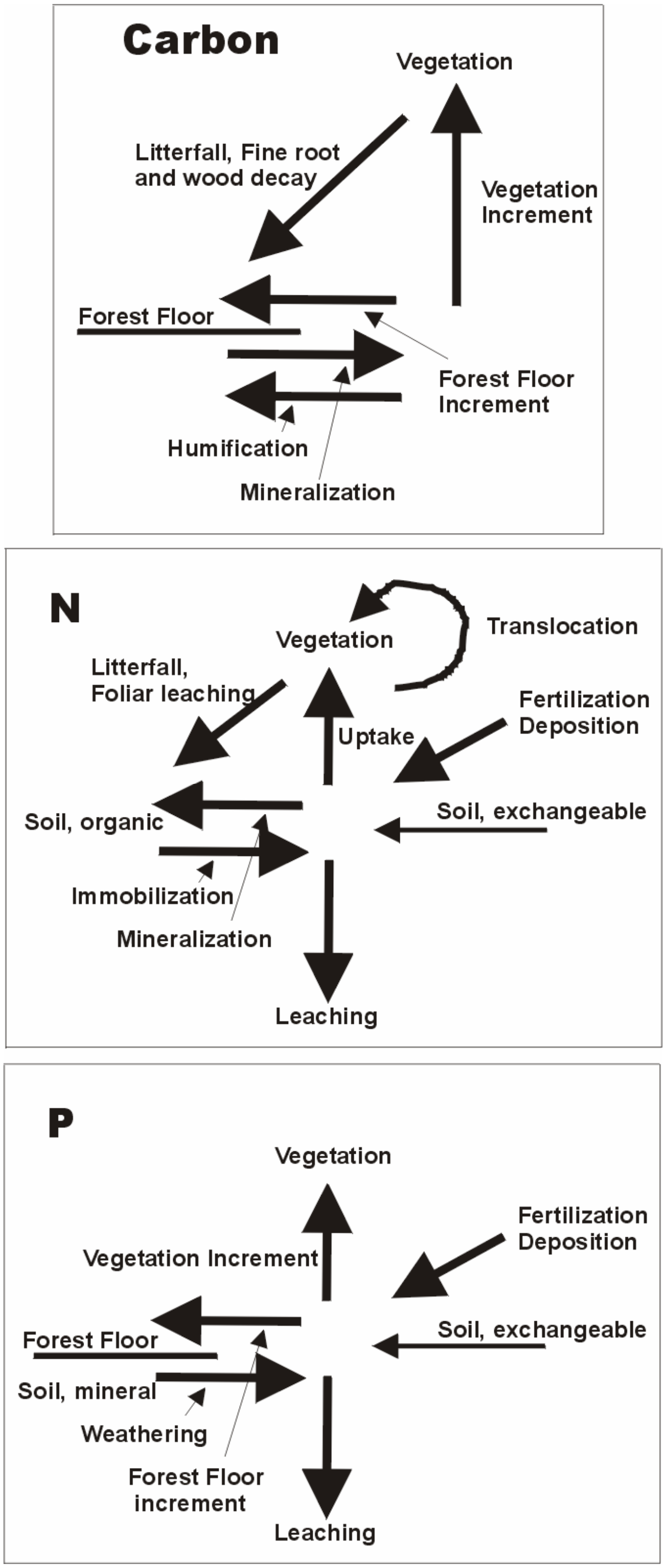


Figure 5.6: Schematic representations of ecosystem fluxes and pools for carbon, nitrogen, and phosphorus as simulated in the NuCSS model (from Verburg and Johnson 2000).

The NuCSS model allows the forest floor C/N and SOM to vary over time based on changes in N mineralization and immobilization rates.

The uptake of N by vegetation is computed as the vegetation N increment minus the amount of N lost in foliage, woody, and fine root litter. Uptake of N for foliage is calculated using the equation:

$$\text{N uptake}_{\text{foliage}} = \text{N}_{\text{foliage}}(t) - \text{N}_{\text{foliage}}(t-1) * (1 - (f_{f->1} * (1 - f_{\text{transl}})))$$

Because exchangeable N in soil rarely exceeds40 kg ha^{-1}, if the total amount of exchangeable N surpasses this amount, the excess will leach (Verburg and Johnson 2000).

The cycling of P in NuCSS differs from N cycling in that weathering of parent material is an additional source of P (Figure 5.6). Also, P mineralization and P in litterfall are not simulated explicitly. Rather, P mineralization is assumed to equal P litterfall.

Input parameters required by the model were derived from the literature and field survey data sources. These parameters include litter decomposition (k-value), which was adjusted to actual evapotranspiration (Table 5.2), plus a series of ecosystem, biogeochemical, and soil properties (Table 5.3). The values used for these analyses were derived to reflect the forest structure and composition, climatic characteristics, foliar and litter chemistry, and soil properties encountered in the different study watersheds (Tables 5.2 and 5.3). The fraction of live leaf material entering the forest floor pool as litter and litter decomposition rates (k-value) were based on the structure and floristic composition

Table 5.2. First-year decomposition (k-value) of leaves of species found in the two study areas.

Species	**k-value**	**Source**	**Source AET**	**Adjusted k-value**	
				Ridge and Valley	**Allegheny Plateau**
A. Rubrum	.5597	Mudrick *et al*. 1994 (WV)	587 (Savage River data)	.5115	.5597
A. Saccharum	.667	Boerner and Rebbeck 1995 (WV)	587 (Savage River data)	.6096	.667
Betula spp.	.4483	Magill and Aber 1998 (Harvard Forest, MA)	578 (Harmon 1992)	.4161	.4553
Carya spp.	.500	default parameter	--	.500	.500
F. americana	.47	Mellilo et al. 1982 (Hubbard Brook, NH)	552 (Harmon *et al*. 1999)	.4568	.4998
K. latifolia	.2148	J. Webster, pers. comm. (Coweeta, NC)	779 (Sun et al. 1999)	.1479	.1619
L. tulipifera	.8965	Mudrick *et al*. 1994 (WV)	587 (Savage River data)	.8193	.8965
N. sylvatica	.5979	Kelly 1973 (TN)	652 (observed 1969-2001)	.4921	.5384
P. rigida	.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon *et al*. 1999)	.1797	.1966
P. pungens	.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon *et al*. 1999)	.1797	.1966
P. strobus	.2173	Andrews experimental forest (OR)	552 (Harmon *et al*. 1999)	.2112	.2311
P. virginiana	.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon *et al*. 1999)	.1797	.1966
P. serotina	.1849	Hubbard Brook, NH (LIDET data)	552 (Harmon *et al*. 1999)	.1797	.1966
Q. alba	.5924	McClaugherty *et al*. 1985 (WI)	535 (McClaugherty *et al*. 1985)	.594	.65
Q. coccinea	.395	Harvard Forest (MA)	578 (Harmon *et al*. 1999)	.3666	.4012
Q. prinus	.3334	Mudrick *et al*. 1994 (WV)	587 (Savage River data)	.3047	.3334
Q. rubra	.395	Magill and Aber 1998 (Harvard Forest, MA)	578 (Harmon *et al*. 1999)	.3666	.4012
Q. velutina	.3323	Magill and Aber 1998 (Harvard Forest, MA)	578 (Harmon *et al*. 1999)	.3084	.3375
R. maximum	.1812	J. Webster, pers. comm. (Coweeta, NC)	779 (Sun et al. 1999)	.1248	.1365
T. canadensis	.3566	McClaugherty *et al*. 1985 (WI)	535 (McClaugherty *et al*. 1985)	.3576	.3913

Table 5.3. Values and sources for input parameters used in NuCSS model simulations run for the seven selected watersheds examined in this study.

Parameter	**Unit**	**Value**	**Source**
Initial Biomass (foliage, branch, bole, coarse and fine roots)	kg/ha	100 for trees 50 for shrubs	model default
Maximum Biomass (foliage, branch, bole, coarse and fine roots)	kg/ha	*Trees*: 8000 foliage	model default
		16000 branch	model default
		80000 bole	model default
		25000 coarse roots	model default
		2000 fine roots	model default
		Shrubs: based on actual biomass estimates	field observations extrapolated using tasseled cap greenness
N, P, K, Ca, and Mg content (foliage, branch, bole, coarse and fine roots)	%	*Trees*: 2.25 foliage N	unpublished data from study areas
		other nutrients	defaults (from Duke Forest, NC)
		K. latifolia: 1.26 foliage N	Monk *et al*. 1985
		.26 wood N	Monk *et al*. 1985
		.17 foliage P	Monk *et al*. 1985
		.11 wood P	Monk *et al*. 1985
		R. maximum: 1.35 foliage N	Monk *et al*. 1985
		.35 wood N	Monk *et al*. 1985
		.13 foliage P	Monk *et al*. 1985
		.10 wood P	Monk *et al*. 1985
N, S, P, K, Ca, Mg, Na, and Cl deposition		N, S, P	J. Lynch (pers comm.)
		K, Ca, Mg, Na, Cl	National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu/)
Fraction N translocated from foliage before senescence	--	.70	model default

Table 5.3, continued

Parameter	**Unit**	**Value**	**Source**
Soil chemical and physical properties	Dekalb soil series		Values for soil layer depths, bulk density, mineral content, CEC, etc. from the NRCS National Lab database (online)
Initial forest floor leaf, woody, and fine root litter weight	kg/ha	0.1	model default
Fraction C in organic matter	--	0.52	W. Currie (pers. comm.)
Decomposition rate constant for leaf, woody, and fine root litter and SOM	fraction/yr	*Leaf:* see Table 5.6 *Wood:* 0.1 *Fine root:* 0.5 *SOM:* 0.001	based on actual forest composition model default model default model default
Fraction humified	--	*Leaf:* 0.2 *Wood:* 0.1 *Fine Root:* 0.1	W. Currie (pers. comm.) W. Currie (pers. comm.) W. Currie (pers. comm.)
Fraction live foliage, branches, and Fine roots entering litter pool annually	fraction/yr	*Leaf:* varies by watershed *Branch:* 0.05 *Fine roots:* 0.5	based on actual forest composition model default model default
Microbial C/N ratio	--	*Leaf:* 0.15 *Wood, fine roots, SOM:* 0.15	model default model default
Microbial carbon use efficiency	--	*Leaf, wood, fine roots, SOM:* 0.15	model default

of the forest canopy (and evergreen understory layer) in each study watershed. Because it was anticipated that differences between model results would be caused primarily by the amount and physical properties of the recalcitrant litter of *K. latifolia* and *R. maximum*, separate litter decomposition rate (k-value) parameters were obtained from the literature for all of the component species of the forests present in the different watersheds examined, and these parameters were adjusted to the actual evapotranspiration (AET) of the two study areas examined. Model defaults were used when no specific value for the watersheds studied were available. This was considered reasonable, as this version of NuCSS was developed for the eastern deciduous biome (P. Verburg, pers. comm.).

In this study, the first run of the NuCSS model for each watershed employed a growth model for canopy trees that used maximal biomass parameters for canopy tree foliar and total aboveground biomass compartments (canopy-only model run). A second run of the model was conducted with a separate growth model for canopy trees and an evergreen understory component using parameters for maximal aboveground and leaf biomass for the evergreen understory community (canopy-with-understory model run). Because the NuCSS model does not limit vegetation growth based on nutrient constraints, the canopy and understory layer vegetation do not compete for available nutrients, nor can they limit each other's growth. Belowground biomass compartments were estimated as the model default 26 percent (24 percent coarse and 2 percent fine root) of the total aboveground biomass for both the canopy and evergreen understory layer vegetation. These values are conservative, but reasonable, estimates for belowground biomass in Appalachian deciduous forests (McGinty 1976).

Leaf Decomposition Data

Leaf litter decomposition rates (k-values) for the component species of forests in the two study areas were obtained from literature sources, adjusted for local climatic conditions, and applied according to the volumetric weighting of the species present in each watershed. The use of scalars to adjust reported decomposition rates is justified by evidence that macroclimate acts as a dominant predictor of leaf litter decay rates, both as a controller of microbial activity and through its influence on litter chemistry (Meentemeyer 1978, Aerts 1997). The adjustment scalar is applied by ratioing the AET of the source area to that of each study area in this work (Table 5.2). A composite decomposition rate was then calculated for the individual watersheds using a weighted average of the specific decomposition rates of all species present. Allometric biomass estimates of leaf weight of individual canopy tree species identified in field surveys (CFI and FIA) were used to estimate the contribution of deciduous canopy tree species, and that amount was divided by two as a conservative estimate of the litter contributions of evergreen conifer tree species (Reich *et al*. 1995). The leaf litter contributions of the evergreen understory was estimated using the previously established leaf biomass estimates, with *K. latifolia* estimates divided by two and *R. maximum* estimates divided by four to reflect their average leaf longevity (Monk *et al*. 1985).

In this study, the first run of the NuCSS model for each watershed employed maximal biomass parameters for canopy tree foliar and total aboveground biomass compartments (canopy-only model run). A second run of the model was conducted using parameters for maximal aboveground and leaf biomass that included the evergreen understory community (canopy-with-understory model run). Belowground biomass compartments were estimated as the model default 26 percent (24 percent coarse and 2 percent fine root) of the total aboveground biomass for both the canopy and evergreen understory layer vegetation. These values are conservative, but reasonable, estimates for belowground biomass in Appalachian deciduous forests (McGinty 1976).

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5.4 Results and Discussion

5.4.1 Aboveground Biomass Estimates

The estimated proportion of the evergreen understory component of the overall forest standing biomass was very small for the two study areas taken in their entirety, but increased a small amount when examined at the level of the selected watersheds (Tables 5.4 and 5.5). Aboveground biomass of the evergreen understory layer was estimated to be less than half of one percent of the overall forest standing biomass in the Ridge and Valley and one percent of the Allegheny Plateau study area.

The leaf biomass estimates of the evergreen understory layer made up a more substantial portion of overall leaf biomass, with total percentage nearly doubling in the Ridge and Valley (.9 percent) and increasing to 5.7 percent in the Plateau. Similar increases in the importance of *R. maximum* (and to a lesser extent *K. latifolia*) leaf biomass as a component of overall forest leaf biomass has been observed by Day and Monk (1977) as having a noteworthy impact on watershed-level nutrient dynamics in the Southern Appalachian Mountains. In the seven watersheds examined in this study, leaf biomass rankings of *R. maximum* (and to a lesser extent *K. latifolia*) among other component species were much higher compared to their overall standing biomass rankings (Table A23). For example, *R. maximum* was ranked 14th (of 25 total species) in total aboveground biomass in the Bluelick Run watershed in the Allegheny Plateau study area,

Table 5.4. Estimated total aboveground and leaf biomass amounts of *Kalmia latifolia* and *Rhododendron maximum* in kilograms and percentages of total forest aboveground and leaf biomass of the forested area within the Ridge and Valley province as well as the Bear Gap Run, Laurel Branch, and Wildcat Run watersheds.

	***R. maximum* Biomass (percent)**		***K. latifolia* Biomass (percent)**		**Total Evergreen Understory Biomass (percent)**	
	Aboveground	**Leaf**	**Aboveground**	**Leaf**	**Aboveground**	**Leaf**
Ridge and Valley Forests	8 X 10^{6} (.06)	1.2 X 10^{6} (.36)	4.51 X 10^{7} (.33)	1.89 X 10^{6} (.57)	5.31 X 10^{7} (.38)	3.09 X 10^{6} (.93)
Bear Gap Run	2.83 X 10^{5} (.21)	4.25 X 10^{4} (1.26)	5.55 X 10^{6} (3.99)	2.32 X 10^{5} (6.86)	5.83 X 10^{6} (4.2)	2.75 X 10^{5} (8.12)
Laurel Branch	2.55 X 10^{5} (.86)	3.83 X 10^{4} (5.05)	8.82 X 10^{5} (2.92)	3.69 X 10^{4} (4.87)	1.14 X 10^{6} (3.78)	7.52 X 10^{4} (9.93)
Wildcat Run	1.74 X 10^{5} (.23)	2.61 X 10^{4} (1.36)	2.83 X 10^{6} (3.59)	1.19 X 10^{5} (6.19)	3.01 X 10^{6} (3.82)	1.45 X 10^{5} (7.56)

Table 5.5. Estimated total aboveground and leaf biomass amounts of *Kalmia latifolia* and *Rhododendron maximum* in kilograms and percentages of total forest aboveground and leaf biomass of the forested area within the Allegheny Plateau province as well as the Big Run, Bluelick Run, Poplar Lick, and Monroe Run watersheds.

	***R. maximum* Biomass (percent)**		***K. latifolia* Biomass (percent)**		**Total Evergreen Understory Biomass (percent)**	
	Aboveground	**Leaf**	**Aboveground**	**Leaf**	**Aboveground**	**Leaf**
Allegheny Plateau Forests	1.19 X 10^{8} (.58)	2.28 X 10^{7} (4.88)	9.38 X 10^{7} (.46)	3.93 X 10^{6} (.84)	2.13 X 10^{8} (1.04)	2.67 X 10^{7} (5.72)
Big Run	2.47 X 10^{6} (.65)	4.72 X 10^{5} (5.19)	2.34 X 10^{6} (.62)	9.8 X 10^{4} (1.08)	4.81 X 10^{6} (1.26)	5.7 X 10^{5} (6.26)
Bluelick Run	3.59 X 10^{6} (1.41)	6.88 X 10^{5} (9.62)	2.47 X 10^{6} (.97)	1.03 X 10^{5} (1.45)	6.07 X 10^{6} (2.37)	7.91 X 10^{5} (11.07)
Poplar Lick	4.3 X 10^{6} (.67)	8.22 X 10^{5} (7.41)	2.84 X 10^{6} (1.01)	1.19 X 10^{5} (1.07)	7.14 X 10^{6} (1.68)	9.41 X 10^{5} (8.48)
Monroe Run	9.27 X 10^{5} (.35)	1.77 X 10^{5} (2.85)	1.42 X 10^{6} (.53)	5.93 X 10^{4} (.95)	2.34 X 10^{6} (.87)	2.37 X 10^{5} (3.8)

but fourth in total leaf biomass due to its thick, sclerophyllous leaves. The promotion in leaf biomass ranking versus overall aboveground biomass ranking was not as great for *K. latifolia* in Bluelick Run (14th and 17th of 25 species respectively). Likewise, in the Poplar Lick watershed in the Allegheny Plateau study area, *R. maximum* ranked 18th (of 25 total species) in total aboveground biomass among the woody species present, but its leaf biomass was the ranked fifth in total leaf biomass among the species identified in the CFI plots within that watershed. For example, *R. maximum* is more important in terms of leaf biomass amount than *Q. prinus* in the Poplar Lick watershed.

5.4.2 Simulation Modeling of Carbon and Nitrogen Pools

The NuCSS model was not designed to test hypotheses regarding specific mechanistic processes associated with nutrient cycling; rather this model was intended to integrate numerous observations, account for pools of C, N, and other nutrients, and perform scenario analysis (Verburg and Johnson 2001). The modifications made on the NuCSS model for this study represents an ideal application of this moderately complex compartment model, in that it facilitates comparisons of amounts and locations of nutrient and carbon storage pools by examining scenarios in which a forest is represented as a canopy-only entity compared to a canopy-with-understory entity.

Before examining differences in NuCSS simulation results for forests modeled as canopy-only and canopy-with-understory, an analysis was performed to assess the sensitivity of the two primary parameters – fraction of live leaf material entering the forest floor annually and the litter decomposition rate (k-value) – that were altered to represent these forest types. This sensitivity analysis was performed for the Bluelick Run watershed in the Allegheny Plateau province, and was designed to compare the k-value and annual fraction of litter from live leaves parameter values used in the canopy-only and canopy-with-understory forests with parameter values that would be used for wholly coniferous and deciduous idealized forest types. This analysis is useful as an illustration of where NuCSS model results for canopy-only and canopy-with-understory forest types lie in the broader range of NuCSS model results defined by extremes in values for these two parameters. The suggested default k-value and annual fraction of litter from live leaves parameter values are both 0.25 for an entirely coniferous forest, and 0.5 and 1.0, respectively, for a purely deciduous forest (Verburg and Johnson 2000). The values used for the k-value and annual fraction of litter from live leaves parameters for the canopy-only model simulation were 0.485 and 0.849, respectively, for the Bluelick Run watershed. The values used in this watershed for the k-value and annual fraction of litter from live leaves parameters for the canopy-with-understory model simulation were 0.471 and 0.786, respectively. The trajectories of the canopy-only and canopy-with-understory forest types closely resemble one another with respect to amounts of C and N accumulated over time, and are bracketed by the idealized deciduous and coniferous forest types (Figure 5.7). The C and N pool sizes in the canopy-only and canopy-with-understory forest types are more similar to the deciduous compared to the coniferous forest type, which is expected considering that the actual forest modeled in the Bluelick Run watershed is dominated by deciduous trees.

Bluelick Run

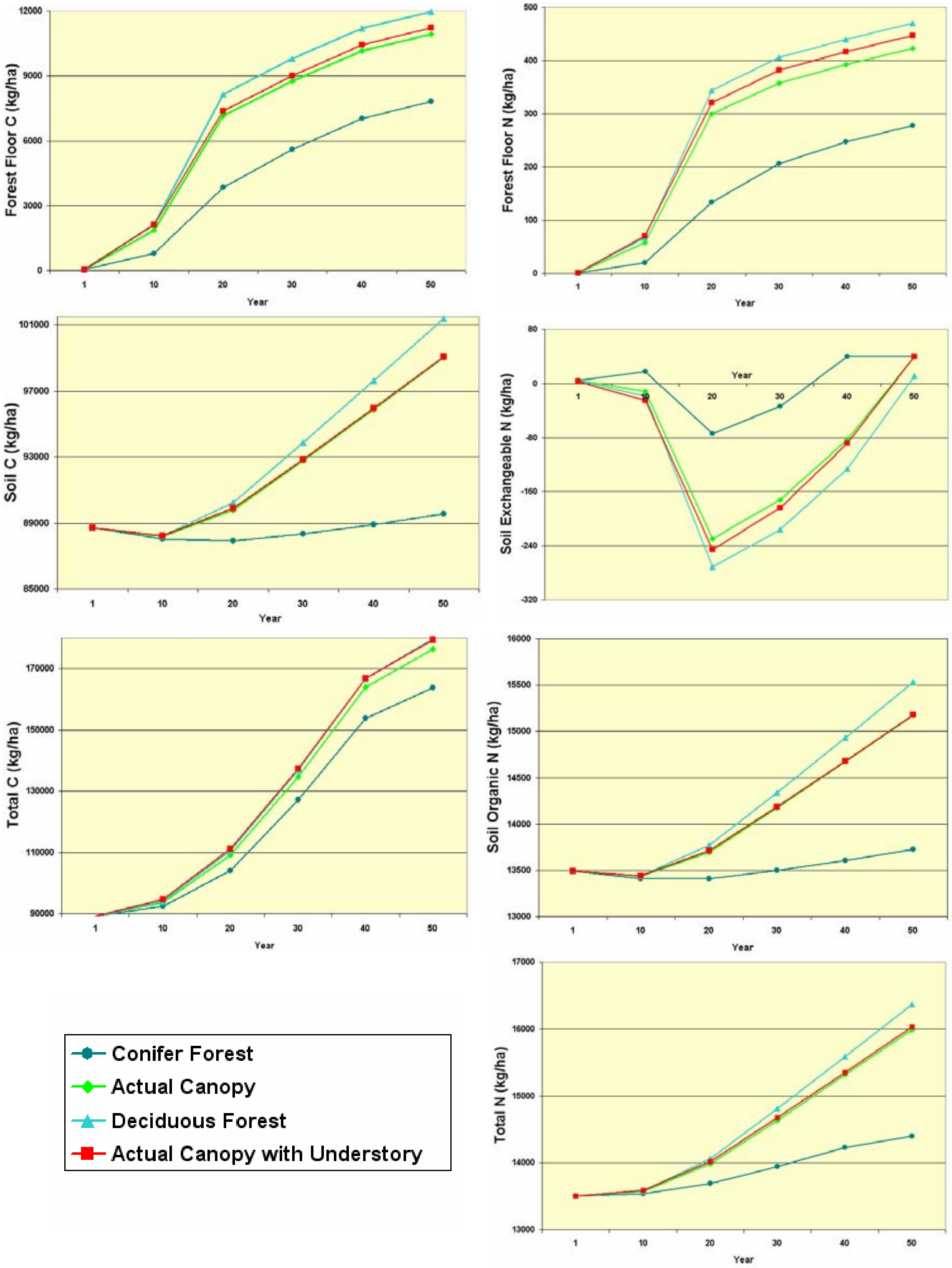


Figure 5.7: Results of sensitivity analysis of the NuCSS model outputs for C and N in the Bluelick Run watershed for a hypothetical purely coniferous, purely deciduous, and the actual floristic composition of the canopy-only and canopy-with-understory forests as developed from FIA and CFI data and field surveys conducted for this research.

The inclusion in NuCSS of evergreen understory communities in simulated forests yielded dramatic increases in the estimated amounts ecosystem carbon sequestration and nitrogen storage. When simulating forests in the test watersheds based only on the composition and biomass of the canopy layer, these forests have between 1631 and 4825 kg/ha less in overall carbon content (Table 5.6) and 41 to 224 kg/ha less nitrogen content (Table 5.7) than if the evergreen understory layer is included.

Differences in the size and location of carbon and nitrogen storage pools were also evident between NuCSS simulations run for forests modeled as canopy-only and canopy-with-understory. The addition of standing and belowground biomass in the form of *K. latifolia* and *R. maximum* in the watershed-scale NuCSS simulations accounted for the largest increases in carbon storage (Table 5.6), followed by gradually increasing pools of forest floor and soil carbon (Figures 5.8 and 5.9). Some of the variability in the soil carbon and nitrogen pools was related to differences in the composition in the evergreen understory layer in the watersheds examined. Specifically, the smallest increases in carbon and nitrogen storage in the canopy-with-understory simulations were observed in the soil pools of watersheds where the biomass of *R. maximum* was highest relative to overall forest aboveground biomass (e.g. Bluelick Run and Laurel Branch). In watersheds where evergreen understory aboveground biomass was dominated by *K. latifolia*, the amount of carbon stored in the soil pool was comparable to that found in the forest floor pool (Table 5.6), whereas the soil pool nitrogen amounts were greater than or equal to that found in the forest floor pool (Table 5.7).

Table 5.6. Size of carbon pools after 50 years of simulation using the NuCSS model for canopy-only forests (Can) and forests with the canopy and evergreen understory communities dominated by *K. latifolia* and/or *R. maximum* (Can+Und).

Watershed	Area (ha)	Total C (kg/ha)	Total C in vegetation (kg/ha)	Total C in soil (kg/ha)	Total C in forest floor (kg/ha)	Total C (kg)
Bear Gap Run (Can)	1308.4	1.81 X 10^5	6.65 X 10^4	1.0 X 10^5	1.42 X 10^4	2.37 X 10^8
Bear Gap Run (Can+Und)		1.85 X 10^5	6.94 X 10^4	1.01 X 10^5	1.5 X 10^4	2.42 X 10^8
Difference		4429	2915	694	820	5.79 X 10^6
Laurel Branch (Can)	287.1	1.81 X 10^5	6.65 X 10^4	1.0 X 10^5	1.42 X 10^4	5.19 X 10^7
Laurel Branch (Can+Und)		1.84 X 10^5	6.9 X 10^4	1.0 X 10^5	1.47 X 10^4	5.29 X 10^7
Difference		3366	2591	270	505	9.66 X 10^5
Wildcat Run (Can)	744.7	1.81 X 10^5	6.65 X 10^4	1.01 X 10^5	1.45 X 10^4	1.34 X 10^8
Wildcat Run (Can+Und)		1.85 X 10^5	6.91 X 10^4	1.0 X 10^5	1.55 X 10^4	1.38 X 10^8
Difference		4825	2641	1148	1037	3.59 X 10^6
Big Run (Can)	1859.6	1.78 X 10^5	6.64 X 10^4	9.99 X 10^4	1.18 X 10^4	3.31 X 10^8
Big Run (Can+Und)		1.8 X 10^5	6.81 X 10^4	1.0 X 10^5	1.2 X 10^4	3.35 X 10^8
Difference		2086	1691	163	232	3.88 X 10^6
Bluelick Run (Can)	1554.8	1.76 X 10^5	6.65 X 10^4	9.9 X 10^4	1.09 X 10^4	2.74 X 10^8
Bluelick Run (Can+Und)		1.79 X 10^5	6.9 X 10^4	9.91 X 10^4	1.12 X 10^4	2.79 X 10^8
Difference		2864	2549	34	281	4.45 X 10^6
Monroe Run (Can)	1271.3	1.78 X 10^5	6.64 X 10^4	9.99 X 10^4	1.21 X 10^4	2.27 X 10^8
Monroe Run (Can+Und)		1.8 X 10^5	6.77 X 10^4	1.0 X 10^5	1.23 X 10^4	2.29 X 10^8
Difference		1631	1210	214	208	2.07 X 10^6
Poplar Lick (Can)	1885.4	1.77 X 10^5	6.65 X 10^4	9.91 X 10^4	1.15 X 10^4	3.34 X 10^8
Poplar Lick (Can+Und)		1.8 X 10^5	6.9 X 10^4	9.94 X 10^4	1.18 X 10^4	3.4 X 10^8
Difference		3104	2493	258	353	5.85 X 10^6

Table 5.7. Size of nitrogen pools after 50 years of simulation using the NuCSS model for canopy-only forests (Can) and forests with the canopy and evergreen understory communities dominated by *K. latifolia* and/or *R. maximum* (Can+Und).

Watershed	Area (ha)	Total N (kg/ha)	Total N in vegetation (kg/ha)	Organic soil N (kg/ha)	Exchangable soil N (kg/ha)	Total forest floor N (kg/ha)	Total N (kg)
Bear Gap Run (Can)	1308.4	16158	351	15336	-103	573	2.13×10^7
Bear Gap Run (Can+Und)		16317	366	15442	-121	630	2.11×10^7
Difference		159	15	106	-19	57	2.08×10^5
Laurel Branch (Can)	287.1	16158	351	15336	-103	573	4.64×10^6
Laurel Branch (Can+Und)		16242	365	15378	-115	615	4.66×10^6
Difference		84	14	41	-12	42	2.42×10^4
Wildcat Run (Can)	744.7	16153	351	15331	-118	588	1.2×10^7
Wildcat Run (Can+Und)		16377	365	15506	-151	656	1.22×10^7
Difference		224	14	175	-33	68	1.67×10^5
Big Run (Can)	1859.6	16134	351	15305	14	463	3.0×10^7
Big Run (Can+Und)		16179	360	15330	1	488	3.01×10^7
Difference		46	9	25	-13	25	8.48×10^4
Bluelick Run (Can)	1554.8	15987	351	15172	40	423	2.49×10^7
Bluelick Run (Can+Und)		16030	365	15177	40	448	2.49×10^7
Difference		43	13	5	0	25	6.74×10^4
Monroe Run (Can)	1271.3	16142	351	15313	0	477	2.05×10^7
Monroe Run (Can+Und)		16183	358	15346	-23	502	2.06×10^7
Difference		41	6	33	-23	25	5.17×10^4
Poplar Lick (Can)	1885.4	16023	351	15197	25	351	3.02×10^7
Poplar Lick (Can+Und)		16101	364	15237	21	364	3.04×10^7
Difference		78	13	39	-4	13	1.47×10^5

Allegheny Plateau Watersheds

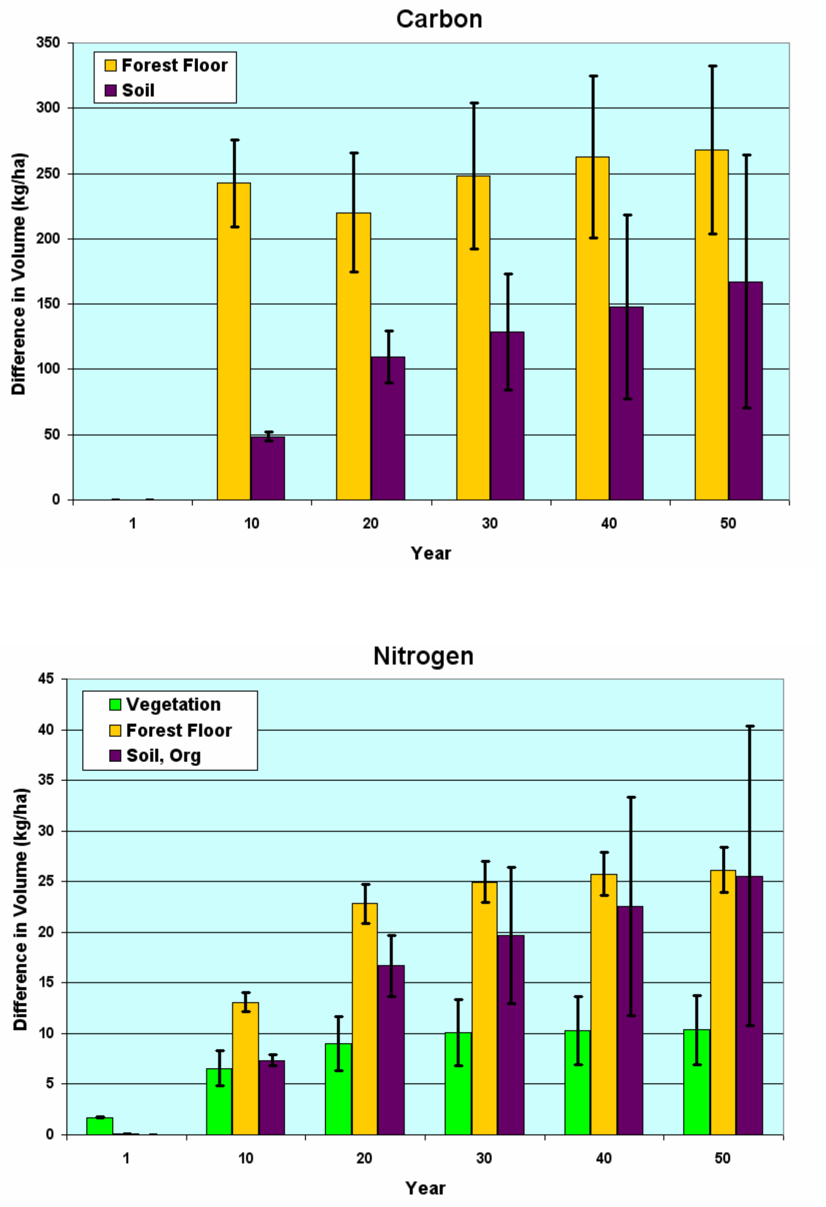
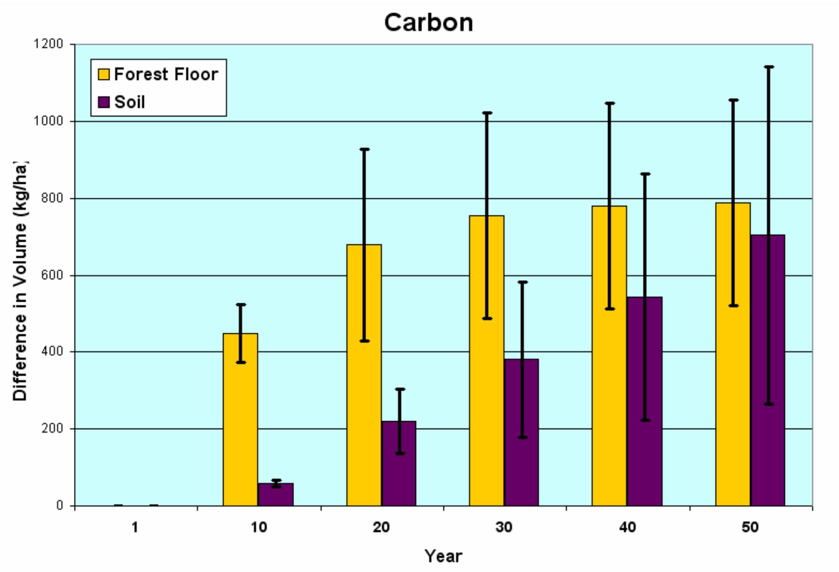


Figure 5.8. Differences between NuCSS model simulation results for carbon and nitrogen storage pools resulting from canopy-only and canopy-with-understory forest input parameters averaged over the four test watersheds examined in the Allegheny Plateau study area.

Ridge and Valley Watersheds



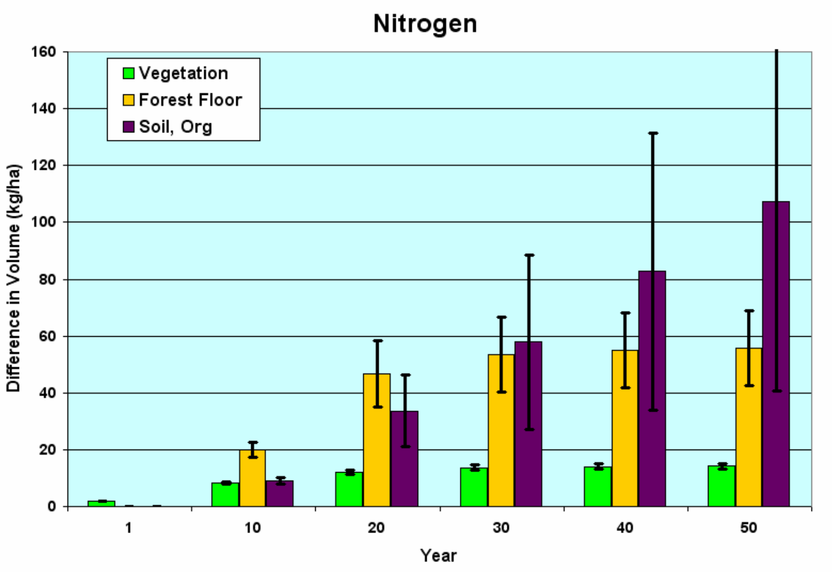


Figure 5.9. Differences between NuCSS model simulations results for carbon and nitrogen storage pools resulting from canopy-only and canopy-with-understory forest input parameters averaged over the three test watersheds examined in the Ridge and Valley study area.

The carbon and nutrient storage capacity of *K. latifolia* and *R. maximum* is greater than their coverage in these forested watersheds suggests. Their sclerophyllous evergreen leaves are higher in biomass than typical of deciduous leaves in Appalachian forests (Day and McGinty 1975). The evergreen habit in which *R. maximum* retains its leaves for an average of four years and *K. latifolia* for two years further expands their capacity to sequester carbon and retain nutrients in their leaf tissue on the watershed scale (Lipscomb and Nilsen 1990). For example, nitrogen uptake by evergreen understory vegetation was estimated by NuCSS to increase by between 6 and 11 kg N ha^{-1} yr^{-1} at year 50 for the canopy-with-understory forest compared to the canopy-only forest. In addition, vegetation pool nutrient storage increased between 2 and 4 percent for nitrogen, and between 2 and 14 percent for phosphorus at year 50 when *R. maximum* and *K. latifolia* were included in the model (Table 5.8). Increases in overall forest carbon and nitrogen pools in *R. maximum* and *K. latifolia* simulations are especially noteworthy in the Allegheny Plateau watersheds where *R. maximum* is more prevalent (Bluelick Run and Poplar Lick compared to Monroe Run), because the relatively larger leaf and overall mass of *R. maximum* compared to *K. latifolia*. Finally, the comparatively large additional storage of phosphorus in forests with *R. maximum* and *K. latifolia* indicated by NuCSS agrees with Thomas and Grigal (1976), who found that P is conserved as a function of high leaf lifespans and the recalcitrant litter produced by these species.

5.5 Conclusions

The NuCSS model was implemented in this study to facilitate the comparison of the sizes of C, N, and P pools when the forest was simulated as a canopy-only or as a canopy-with-

Table 5.8. Amount of additional carbon, nitrogen, and phosphorous (kg/ha) added to the total vegetation pools (standing and belowground biomass) at year 50 by including *K. latifolia* and *R. maximum* to the forests simulated for NuCSS model runs in the seven watersheds. The parenthetic percentages indicate the addition to simulated forest vegetation pools by including *K. latifolia* and *R. maximum*.

Watershed	**Aboveground Biomass**	**Carbon**	**Nitrogen**	**Phosphorus**
	Ridge and Valley			
Bear Gap Run	4458.3 (4.2)	2914.9 (4.2)	15.2 (4.1)	2.3 (5.5)
Laurel Branch	3961.5 (3.8)	2590.6 (3.8)	13.5 (3.7)	2.1 (4.9)
Wildcat Run	4039.5 (3.8)	2640.8 (3.8)	13.8 (3.8)	2.1 (5)
	Allegheny Plateau			
Big Run	2585.9 (1.3)	1691.3 (2.5)	8.8 (2.4)	1.4 (3.2)
Bluelick Run	3901.4 (2.4)	2549.1 (3.7)	13.3 (3.6)	6.04 (14.2)
Monroe Run	1844.4 (.9)	1210.2 (1.8)	6.3 (1.8)	1 (2.3)
Poplar Lick	3785.5 (1.7)	2492.6 (3.6)	13.1 (3.6)	2 (4.7)

understory. Although NuCSS is not the most complex ecosystem model, predictions of overall C and N sequestration in the simulated forests simulated using this model are comparable to sequestration amounts obtained elsewhere. For example, the sequestration rates of forests growing on abandoned farmland in Rhode Island were found to be similar in estimated overall C ($1.75 \text{ X } 10^5$ kg ha^{-1}), with comparable proportions of C in the vegetation, soil, and forest floor pools for the central Appalachian forest (Table 5.6) and the Rhode Island forest (Hooker and Compton 2003). However, the N sequestered after 50 years (5400 kg ha^{-1}) by the Rhode Island forests was only about one third what was predicted by the NuCSS model (Table 5.7). This difference was due to much lower soil N in the Rhode Island forest compared to the central Appalachian forest (approximately 16000 compared to 4500 kg ha^{-1}, respectively), which may be accountable by differing soil types, with the former being glacial till derived. However, the size of the N pools in the vegetation (400) and forest floor (500) were comparable for these two forests (Hooker and Compton 2003). It should be noted that the precision of the results reached using NuCSS are not at issue for this research, because the comparison of NuCSS results for canopy-only and canopy-with-understory are not adversely affected by the lack of precision in some of the parameter settings. The results of the NuCSS simulations showed that additions to the overall C, N, and P pools in the modeled watersheds were larger than that accounted for by the addition of the evergreen understory vegetation biomass alone, with noteworthy increases in the forest floor and soil pools (Tables 5.6, 5.7, and 5.8). These results were obtained by changing only parameter inputs related to vegetation biomass, annual proportional litter contributions, and decomposition rates to simulate the characteristics of canopy-only and canopy-with-understory forest types.

The results obtained from NuCSS show increases in carbon sequestration and nutrient storage that are significant at the scale of the watershed, and may act to mitigate the effects of certain disturbances such as gypsy moth defoliation. For example, when the effects of this disturbance was examined in the Big Run watershed, stream discharge of N increased to indicate an export of about 3 kg N ha^{-1} yr^{-1} (Eshleman *et al.* 1998, Eshleman 2000), which is roughly half of the annual N deposition of 6.02 kg N ha^{-1} yr^{-1} in the Allegheny Plateau region. Similarly, Lovett *et al.* (2000) found that stream export of N in gypsy moth defoliated watershed in Virginia and West Virginia was roughly half of the 8 kg N ha^{-1} yr^{-1} annual N deposition. In this research, NuCSS results for the Big Run watershed indicate that the addition of the evergreen understory layer increased N mineralization by 7.8 kg N ha^{-1} yr^{-1} and vegetation uptake by 7.5 kg N ha^{-1} yr^{-1}. The soil and forest floor pools stored an additional 0.3 kg N ha^{-1} yr^{-1}. Likewise, in the Poplar Lick watershed N mineralization increased by 7.9 kg N ha^{-1} yr^{-1}, vegetation uptake increased by 7.1 kg N ha^{-1} yr^{-1}, and the soil and forest floor pools increased by 0.8 kg N ha^{-1} yr^{-1} due to the inclusion of the evergreen understory. This additional N throughput and storage may have enough of an influence on the watershed scale to attenuate N leakage caused by gypsy moth defoliation, especially if most of the N released during this disturbance is in fact redistributed from the canopy to other ecosystem pools such as the forest floor (Lovett *et al.* 2000). Also, the evergreen understory would not experience mortality after such an event, but rather may benefit from the redistribution of nutrients.

The capacity of North American forests to act as carbon sinks is considered important in strategies for reducing some atmospheric greenhouse gases (Sedjo 1992, Myneni *et al.* 2001), and a number of estimates of forest carbon and nutrient storage capacity on the regional and continental scales have been enabled by the use of remote sensing (Potter 1999, Myneni *et al.* 2001). In a number of these investigations, estimates of carbon and nutrient storage capacity were found to be sensitive to regional differences in dominant life form (coniferous or broad leaved) and species composition (Fan *et al.* 1998, Myneni *et al.* 2001). Similarly, this study points out the regional relevance of the evergreen understory layer in carbon and nutrient storage in Appalachian forests. While regional C pool added by the presence of evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* in these central Appalachian forests does not even come close to accounting for the "missing" C in global budgets, the results of this study suggest that these communities are an integral part of the functioning of Appalachian forests. This may be especially true for southern Appalachian forests, where increased rainfall and moisture availability may contribute to more ideal growing conditions for *R. maximum*, hence increasing the importance of evergreen understory vegetation as a component of forests in that region (White *et al.* 2001). For example, the evergreen understory component of a 50 year old forest growing in the Coweeta watershed 18 in the southern Appalachians was found to be 8.8 percent of the overall forest aboveground biomass (12,344 kg ha^{-1} out of 139,900 kg ha^{-1}) (Day and Monk 1974). As such, a detailed accounting of the species present in the understory as well as the canopy of Appalachian forests through the integration of field survey data and classified remote sensing data is quite valuable.

The carbon and nutrient storage potential of the evergreen understory layer is small but in places considerable. Forest managers and others involved in land use management should therefore consider the capacity of such forests to retain additional C and nutrients when evaluating active landscape management plans. Whereas the presence of thickets of *R. maximum* and *K. latifolia* in forest understories has been found to inhibit canopy tree regeneration and therefore lead to declines in timber output (Minkler 1941, Neary *et al*. 1984, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Nilsen *et al.* 2001, Walker *et al*. 1999), these species also account for a larger amount of the carbon and nutrient component of forests than their physical presence suggests, and thus may be important with respect to water quality maintenance (Yeakley *et al*. 1994). Specifically, abundant evergreen understory vegetation on the watershed scale such as that found in the Allegheny Plateau might be partially able to attenuate stream nitrate export response to gypsy moth defoliation (Eshleman *et al*. 1998, Eshleman 2000). In addition, their carbon and nutrient storage capacities may meaningfully contribute to the air quality maintenance and climate change mitigation services provided by Appalachian forests. The trade-off involved in removing evergreen understory species to maximize timber output should be balanced against their role in the overall functioning of the forest with respect to other important societal services.

Chapter 6: Summary and Conclusions from Research into Evergreen Understory Layer Characteristics in Central Appalachian Forests

6.1 Introduction

North American forest ecosystems provide several societal services, including the maintenance of air and water quality, sediment trapping, flood attenuation, nutrient and carbon storage, acting as a source of wood products, and habitat and refuge for wildlife (Schlesinger 1977, Sedjo 1992, Daily *et al*. 1997, Perry 1998, Aber et al. 2000, Myeni *et al*. 2001, Currie et al. 2003). In the eastern United States, the Appalachian highlands region contains perhaps the most extensive contiguous area of temperate deciduous forest ecosystems, since the high amount of topographical relief has historically precluded their large-scale transformation into agricultural or urban land uses (Robison 1960). The large area of predominantly forested land cover in the central Appalachian highlands has been cited as being especially important in protecting the water supply for middle Atlantic urban areas in the Chesapeake Bay watershed (Altman and Parizek 1995, Lowrance *et al.* 1997, Eshleman *et al*. 2000).

The evergreen understory species rosebay rhododendron (*Rhododendron maximum* L.) and mountain laurel (*Kalmia latifolia* L.) dominate the understory layer in Appalachian forests in localized areas. These broadleaf evergreen species enhance the functioning of Appalachian forest ecosystems with respect to the provision of societal services, because they have the potential for slowing mineral cycling (McGinty 1972, Thomas and Grigal 1976, Monk *et al.* 1985), and therefore may have water quality maintenance implications in the event of disturbance. They are also significant components of Appalachian forests with regard to carbon sequestration and nutrient budgets (McGinty 1972, Thomas and Grigal 1976, Monk *et al*. 1985). Evergreen understories dominated by these species also provide forage and refuge for wildlife (Romancier 1970, Gates and Harman 1980, Thackston *et al*. 1982, Johnson *et al*. 1995, Spear 1998, USDA 2002), and enhance the beauty and hence inspirational value of Appalachian forests (Hollenhorst *et al*. 1993);

In contrast, the presence of evergreen understory communities dominated by *R. maximum* and/or *K. latifolia* inhibits canopy tree regeneration when present in dense stands (Minkler 1941, Phillips and Murdy 1985, Clinton *et al.* 1994, Waterman *et al.* 1995, Clinton and Vose 1996, Baker and Van Lear 1998, Nilsen *et al.* 1999, Walker *et al*. 1999, Beckage *et al.* 2000, Nilsen *et al.* 2001, Lei *et al*. 2002, USDA 2002). This effect may be a particularly acute in upslope xeric and dry-mesic areas (Waterman *et al*. 1995, Waldrop *et al*. 2000), and in riparian areas (Baker 1994, Hedman and Van Lear 1995, Baker and Van Lear 1998, Vandermast and Van Lear 2002).

Examination of the spatial extent and temporal dynamics of *K. latifolia* and *R. maximum* in Appalachian forests is worthwhile, because they are inadequately documented, yet are significant with respect to carbon sequestration and nutrient cycling on the landscape scale, and are therefore important components of these forests' overall capacity to mitigate climate change and maintain water quality. In addition, the temporal dynamics of both leaf area (density) and spatial extent of the evergreen understory layer is relevant to its role in the inhibition of canopy tree regeneration, and hence the sustainability of the structure and function of Appalachian forest ecosystems for various ecological, societal, and aesthetic values. As such, any holistic forest management plan must be designed such that the positive and negative effects of the evergreen understory layer in terms of forest ecosystem functioning are balanced. Luckily, feasible strategies to accomplish this are a very real possibility in the forests of the central Appalachian highlands region.

The approach followed in this study utilized the unique natural laboratory embodied by two geographically adjacent, but physiographically distinct study areas. By comparing and contrasting study areas located in the Ridge and Valley and the Allegheny Plateau provinces of the central Appalachian highlands, differences in forest ecosystem characteristics related to climatic characteristics, geology and geomorphology, land use history, and disturbance history can be examined. Moreover, this region lacks baseline data on the spatial extent, biomass amount, and landscape scale ecological impacts of evergreen understory communities dominated by *K. latifolia* and *R. maximum*.

6.2 Review of Findings

In the course of this research, various aspects of the spatial distribution, growth habits, and ecological roles of *K. latifolia* and *R. maximum* in the forests of the central Appalachian highlands were examined. Chiefly, evergreen understory communities dominated by *K. latifolia* and/or *R. maximum* were not found in large portions of the two study areas examined, but their distribution was found to be correlated with land use, disturbance gradients, and geological parent material in the Ridge and Valley province, whereas topographic gradients proved to be a better predictor of their distribution in the

Allegheny Plateau. Second, simplified forest vertical structure was associated with the presence of an evergreen understory layer. Specifically, open midstories were significantly related to the presence of continuous evergreen understory layers, supporting the proposition that evergreen understory layers inhibit canopy tree regeneration. Also, timing in the oscillation of growth vigor of the evergreen understory layer was temporally associated with climatic fluctuations and gypsy moth defoliations. Finally, evergreen understory vegetation accounted for a surprisingly large proportion of the carbon and nutrient storage pools in watersheds selected for intensive study. A more detailed discussion of these findings is organized by chapter below.

In Chapter 2, a significant correlation was found between the presence of evergreen understory communities dominated *R. maximum* and/or *K. latifolia* and midstory volume, hence a simplification of forest structure that could be tied to inhibition of canopy tree regeneration (Baker and Van Lear 1998). Also, *K. latifolia* understory communities were found to favor poorer sites with open tree canopies characterized by lower basal area in the Ridge and Valley province, and leaf area in both physiographic provinces studied (*sensu* Wilson and O'Keefe 1983). Ordination analysis reinforced the conclusions encountered in numerous literature sources that topographic gradients are the strongest explanatory factor for the distribution of both *R. maximum* and *K. latifolia* in the Allegheny Plateau region (Lipscomb and Nilsen 1990a, 1990b, Muller 1991). However, land use and disturbance (gypsy moth defoliation) gradients were the most strongly related factors of those examined for the distribution of *K. latifolia* in the Ridge and Valley province. Finally, the canopy tree basal area in locations with a *K. latifolia* understory that were previously infested by gypsy moth was found to be significantly lower than areas that contained no evergreen understory, suggesting a comparative shortfall in canopy tree recovery in these areas.

Methods for accurately mapping the spatial extent of *R. maximum* and *K. latifolia* were explored in Chapter 3. This was necessitated by the lack of an existing land cover classification in which the spatial distribution of the evergreen understory is accurately characterized. For example, the 1992 National land cover dataset (NLCD) only maps forest cover to Anderson level II, with forest cover classes of deciduous, evergreen, or mixed. These classes describe tree canopy characteristics and do not enlighten the user as to the understory attributes of these Appalachian forests. The developers of the NLCD concede that this classification scheme cannot satisfy every research goal due to differences between regional vegetation assemblages, and that users must at times develop land cover information *tabula rasa* from primary data sources (Vogelmann *et al*. 2001). Given the importance of evergreen understory layers dominated by *R. maximum* and/or *K. latifolia* in Appalachian forests, this qualifies as such a scenario. It is anticipated that primary (Landsat) data sources will be delivered as a component of the 2000 NLCD product to better support such user needs (Vogelmann *et al*. 2001).

Using inexpensive and readily available leaf-off Landsat TM image data, evergreen understory layer communities were found to be distinguishable at an accuracy level of greater than 80 percent. In addition, topographic information was found to be useful for increasing classification accuracy in the Allegheny Plateau, where land use history was not as intense as in the Ridge and Valley province, and potential vegetation communities (i.e. evergreen understory communities) are realizing their niches with greater predictability. Also, the use of decision trees enabled the identification of Landsat bands and derivatives as well as topographic variables that are particularly useful in identifying and parsing out different evergreen understory community types. In the study area delimited within the Allegheny Plateau province, evergreen understory communities are present in 26 percent of the total forested area (15 percent dominated by *K. latifolia*, 10 percent dominated by *R. maximum*, and 8 percent mixed). In the Ridge and Valley province, evergreen understory communities are present in only 6 percent of the forested areas (almost all dominated by *K. latifolia*), but coverage is locally important in specific watersheds.

Growing season hyperspectral image data (AVIRIS and EO-1 Hyperion) did not prove to be as useful as Landsat image data in mapping evergreen understory communities. However, the combined use of leaf-off EO-1 Hyperion and Landsat image data is a fruitful future research approach to pursue so that the confusion between understory hemlock and the broadleaf evergreen understory species *K. latifolia* and *R. maximum* in the Allegheny Plateau study area can be resolved. The EO-1 satellite platform which carries the Hyperion hyperspectral imaging instrument follows one minute behind the Landsat space vehicle along the same orbital path, allowing it to image an areal footprint on the ground that coincides with the central 7.7 km strip of the 185 km swath width of the Landsat ETM imager. Moreover, the price for this image data is in the same relatively inexpensive range of Landsat TM image data, having recently been reduced to

250 USD for an archived scene. However, suitable data availability is a limiting issue. For example, a search for available leaf off EO-1 Hyperion data yielded only one image (March 31, 2003) for this study area, but unfortunately this image was marred by greater than 60 percent cloud cover.

The results from Chapters 2 and 3 provided the basis to ask questions about the spatial and temporal dynamics of evergreen understory communities in the Mid-Atlantic Highlands. Chapter 4 presents a novel combination of remote sensing and dendrochronology to track the growth vigor of forest evergreen understory communities dominated by *K. latifolia* and/or *R. maximum*. This method facilitated a multiscale approach to examining the growth responses of understory shrubs to climatic fluctuations and gypsy moth defoliation. Specifically, the combination of an archive of yearly growth vigor measures from annual increments at the scale of the individual was compared to synoptic observations at the landscape scale from remote sensing. Although the spatial extent of the evergreen understory did not change over the 16-year time series of satellite imagery, *K. latifolia* and *R. maximum* did exhibit notable fluctuations in growth vigor during this time period. Comparisons of data from the two physiographic provinces showed that the growth rate of *K. latifolia* was not noticeably influenced by the difference in precipitation amount between the two zones. Whereas the growth rate of *R. maximum* was increased by the moister conditions present in the Allegheny Plateau relative to the Ridge and Valley province, *K. latifolia* growth rates were identical for both provinces.

By tracking the leaf area expansion and contraction of the evergreen understory layer in areas experiencing canopy disturbance and climatic fluctuation, this research suggests that at least two mechanisms potentially allow successful regeneration of canopy trees in evergreen understory areas – sporadic death among *K. latifolia* individuals and variability in the growth vigor (and hence leaf area) of *K. latifolia* and *R. maximum*. It is apparent from field observations that there is currently a considerable amount of mortality among *K. latifolia* individuals, especially in the Allegheny Plateau. Sporadic mortality of individual shrubs is not unusual in *K. latifolia* understories, especially considering the relatively young average age of *K. latifolia* individuals harvested in the two study areas (range 16 to 45 years averaging 28 in the Ridge and Valley, and 13 to 49 averaging 28 in the Allegheny Plateau). Catastrophic disturbances such as fire have not occurred since the last harvest in the areas from which *K. latifolia* was collected, so one would expect a more mature age structure in this sample unless individuals die and are replaced on a regular basis. In contrast, *R. maximum* appears to be rather long-lived in these study areas, with ages ranging from 15 to 80 years (averaging 33) in the Allegheny Plateau and ranging from 40 to 90 years (averaging 58) in the Ridge and Valley study area. In addition, changes in the leaf area of *K. latifolia* and *R. maximum* were apparent both on the landscape scale in the remote sensing change detection results and at a finer scale in the dendrochronology analyses, thereby affirming the working hypothesis that evergreen understory communities dominated by *K. latifolia* and *R. maximum* are persistent on the landscape scale, but variable over time at the scale of the individual.

Variations in leaf area and growth vigor of these species also correspond to the occurrences of climatic fluctuations and gypsy moth disturbance. The localized scale and individualistic nature of changes in growth vigor were especially evident in the dendrochronology results. On the landscape scale, both the *K. latifolia* and *R. maximum* communities in the Ridge and Valley province experienced a larger degree of greening up between 1984 and 2000 compared to the evergreen understory communities in the Allegheny Plateau province. The ‘mixed’ evergreen understory communities in the Plateau actually experienced a net browning down, except in topographically wet areas. It was apparent that gypsy moth activity had an overall negative effect on the growth vigor of *K. latifolia* in the Ridge and Valley province over the long term (1984 and 2000), but short-term gains in greenness were seen in the remote sensing data directly after infestations. The results of this portion of the overall research suggest that regeneration bottlenecks potentially caused by dense evergreen understory layers should only exist in very localized areas that are ideal for *R. maximum* and/or *K. latifolia* growth that also have not experienced large perturbations. However, notable inhibition of canopy tree regeneration would not be expected over the entire area wherein these understories exist.

Following Chapters 2-4, the question remained: what is the overall effect of the evergreen understory layer on Central Appalachian forest ecosystems? Insight into this question was gained in Chapter 5 by modeling carbon and nutrient pools in Appalachian Forests both including the evergreen understory layer and excluding it (as all current models do). The results of the work in the earlier chapters were thereby used to more completely characterize the importance of species composition and structure of forest communities to carbon and nutrient storage and cycling dynamics (Fan *et al.* 1998, Myneni *et al*. 2001). In particular, carbon storage potential of the evergreen understory is of concern because forests are viewed as important sinks potentially capable of mitigating increases in atmospheric carbon concentrations. Their nutrient storage and cycling dynamics are consequential to these forests' overall capacity to support water quality maintenance, particularly in the event of large scale disturbances (Eshleman and Morgan 1998, Lovett *et al*. 2002, but see Yeakley *et al*. 2003).

The carbon sequestration and nitrogen and phosphorus storage potentials of *K. latifolia* and *R. maximum* were investigated by first estimating their aboveground biomass, then running a 50-year simulation on the forests present in several watersheds to examine specific disparities between forests represented as a simple canopy-only forest stand and as a canopy-with-understory forest. The foliar portion of overall aboveground biomass in these evergreen understory species (especially *R. maximum*) were of greater importance compared to their overall standing biomass rankings among all species present. The leaf biomass of *R. maximum* and *K. latifolia* was between 7.6 and 9.9 percent of the total leaf biomass in the three watersheds examined in the Ridge and Valley province and between 3.8 and 11.1 percent of the total watershed leaf biomass in the four watersheds examined in the Allegheny Plateau province. Moreover, their aboveground standing biomass accounted for merely a portion of the carbon sequestered and nitrogen stored by *R. maximum* and *K. latifolia* in the forest ecosystems studied at the watershed scale. Notable increases in the carbon and nitrogen amounts in the forest floor and soil pools were also found in forests modeled as a tree canopy combined with an evergreen understory layer. Carbon storage increased by between 1631 and 4825 kg/ha after 50 years with the addition of evergreen understory layer vegetation in the simulated forests. Nitrogen storage increased by between 41 and 224 kg/ha as a result of the addition of the evergreen understory. Nitrogen storage predominated in the forest floor compared to the soil pool when a larger amount of *R. maximum* was present in a watershed, most likely due to the larger amounts of recalcitrant litter produced annually by this species compared to *K. latifolia*. Finally, storage of phosphorus in *K. latifolia* and *R. maximum* was found to be greater than their watershed-scale standing biomass amounts would suggest.

The potential characteristics and developmental trajectories of four hypothetical forest archetypes may be conjectured upon as a means to synthesize the results of this research. Four archetypal forests serve as heuristic devices: Disturbed (gypsy moth) no understory, not disturbed no understory, disturbed (gypsy moth) with understory, and not disturbed with understory.

In the disturbed (gypsy moth) no understory type, canopy trees that are present in the regeneration layer and/or midstory are able to take advantage of canopy gaps produced from tree mortality after severe gypsy moth defoliation events. As a result, the forest canopy is more well developed (higher BA and LAI), and the vertical structure is more complex compared to areas where an evergreen understory is present. Red maples may perhaps be more dominant below the canopy layer compared to forests with an evergreen understory present, due to less competition for nutrients and water which would inhibit their growth in the seedling and sapling stages. Red maple may potentially become a dominant canopy tree if extensive canopy mortality occurs.

Forest vertical structure is also more complex in the not disturbed no understory forest type compared to forested areas where an evergreen understory is present, with a well developed midstory layer and canopy replacing trees present in the regeneration layer (e.g. seedling and ‘pole’ trees) as well as the midstory layer. Red maple may be present in higher numbers compared to forest types with an evergreen understory component, but should remain in the understory as long as canopy replacing disturbance events do not occur.

In the disturbed (gypsy moth) with understory forest type, the lack of well developed midstory layer due to regeneration failure of canopy trees may lead to a dominance of the evergreen understory layer, with a very open forest (low BA and LAI) above the evergreen understory - hence a exceedingly simple vertical forest structure - if disturbance is sufficiently severe and/or temporally continuous. However, the evergreen understory may contribute to an attenuation of nutrient leaching associated with occasional gypsy moth defoliation when gypsy moth infestation is less severe and does not lead to extensive canopy (host) tree mortality.

Finally, in the not disturbed with understory forest type, the evergreen understory layer may contribute to a lack of regeneration below the canopy if its coverage is sufficiently continuous. In addition, forest vertical structure may be less complex than evergreen understory-free areas, with a less well-developed midstory layer caused by canopy tree seedling inhibition if evergreen understory is sufficiently continuous. Finally, after the evergreen understory layer has adequately established (e.g. after about 20 years), this layer will be responsible for notable increases in the amount of biomass in the soil and forest floor in addition to the aboveground and belowground biomass added by the vegetation itself. These increases will enhance the nutrient and carbon sequestration services performed by this forest type.

6.3 Management Implications

Forest ecosystem management has been referred to as a ‘wicked’ problem for which no single correct solution or stopping rule exists (Rauscher 1999). Methods typically employed for ‘tame’ problems (using science and technology) have a tendency to break down because of the human dimension to forest ecosystem management, which arises from the competing demands of deriving economic versus ecosystem services from forests. As such, it is difficult to recommend a single management prescription for the forests of the Central Appalachian highlands based on the findings of this research. Rather, this work presents some useful methods for determining the spatial extent and biomass magnitude of the evergreen understory component of these forests and suggests their impacts (”positive” or “negative,” depending on the management objective) on its structure and functioning. These findings are not intended to represent the sole basis of a management or restoration plan, but interactions between the inhibitory effects of evergreen understory vegetation and other factors that influence tree seedling recruitment (seed dispersal, gap phase regeneration, etc.) should be considered in overall forest management strategies, as they affect the floristic and structural attributes of Appalachian forest (Rivers *et al*. 1999, Beckage *et al*. 2000, Nilsen *et al*. 2001, Lei *et al*. 2002, Vandermast and Van Lear 2002, Lambers and Clark 2003). In addition, the carbon and nitrogen storage and nutrient cycling impacts of evergreen understory communities need to be acknowledged. Specifically, influences of evergreen understory vegetation communities that are seen as favorable and unfavorable to the desired functioning of Appalachian forest ecosystems need to be weighed into any management plan.

Attempting to re-establish what is imagined to be the pristine condition of the forests of the central Appalachian highlands is not a realistic restoration or management goal. Numerous internal and exogenous forces affect regional forests, and change as societal needs and environmental conditions change. Restoration and conservation goals are therefore moving targets. For example, the forests of this region are now fragmented, the atmospheric deposition of nitrogen and other nutrients is greater than ever before, climatic regimes are potentially undergoing change (Figure 6.1), traditional fire regimes have been altered, and an invasive pest (gypsy moth) has introduced a novel and rather destructive disturbance regime to these forests. The oak component of these forests may be under an inordinate amount of stress due to the cessation of fire and the introduction of the gypsy moth, resulting in their replacement by other species due to their competitive advantages over oaks under current conditions (Lorimer *et al*. 1994, Musika and Liebhold 1999). Indeed, the suppression of fire in the 20th century is an often-cited rationale for the decline of oaks in the eastern deciduous forest biome of North America (Abrams 1992, 2003, Shumway *et al*. 2001, MacDonald *et al*. 2003). In part, this is because oaks are more fire tolerant than many forest tree species, such as *Acer rubrum* (Abrams 1998), and have lost this relative advantage to other species during the era of fire suppression.

The traditional role of *R. maximum* and *K. latifolia* in these forests is likewise difficult to estimate and impractical to restore. We know from historical accounts that the evergreen understory was present – and in places quite dense – in this region hundreds of years ago (Robison 1960), and it is apparent from this research that the growth vigor of *R. maximum* and *K. latifolia* is variable over time. The apparent trend of milder winters (Figure 6.1), the cessation of traditional fire regimes, and the recurrence of gypsy moth defoliation may have provided relative advantages to these evergreen understory species. This, in turn, may be actively altering the overall structure and functioning of the forests of the central Appalachian highlands. Specifically, the inhibitory influence of *K. latifolia* and *R. maximum* on canopy tree regeneration in forest understories appears to be increasing, potentially leading to their spatial expansion in these forests. While the evergreen understory layer may act as a valuable buffer enhancing the nutrient retention capacity of forests in this region, their regeneration inhibition potential is of concern to forest managers.

The decline of oak species is a central issue facing forest managers of the deciduous forests across the eastern United States (Abrams 1992, 2003, Lorimer *et al*. 1994, Macdonald *et al*. 2003), and the role of the evergreen understory should be considered in any effort to sustain desired oak proportions in Appalachian forests. The spatial and environmental context of the relevant species is critical to such an assessment. *K.*

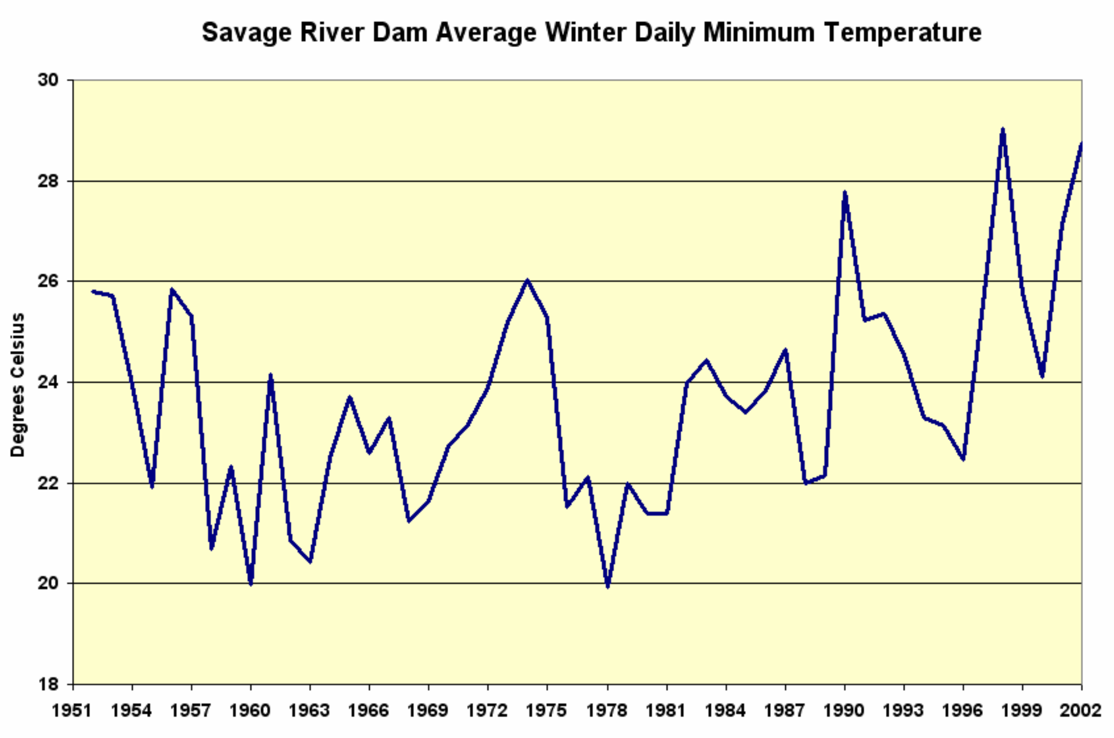


Figure 6.1: Winter averages (Nov-March) of daily minimum temperature readings collected at the Savage River Dam station (NCDC station ID #188065). Note the apparent trend towards higher average daily minimum temperatures during the 1980s and 1990s.

latifolia exhibits reduced photosynthetic performance and water use efficiency under low irradiance conditions (Lipscomb and Nilsen 1990b), whereas *K. latifolia* stem growth under higher light conditions has been found to be three times that observed under low light conditions (Davidson 1966). As such, *K. latifolia* typically grows on more exposed sites in Appalachian forests compared to *R. maximum*, such as upper slopes and ridge tops (Monk *et al.*1985, Lipscomb and Nilsen 1990a, 1990b, Muller 1991), The typical topographic position inhabited by *K. latifolia* on the landscape therefore coincides with various upland oak species, which are not considered shade tolerant (Abrams 1992, 2003), and are consequently inhibited in their development from seedling into sapling stages by the shade cast by tall understory vegetation such as *K. latifolia* (Lorimer *et al*. 1994, Nilsen *et al*. 2001, Abrams 2003, MacDonald *et al*. 2003). In addition, the cessation of fire in Appalachian forests is associated with the expansion of *R. maximum* upslope from riparian areas, forming large thickets where canopy tree seedlings are inhibited and forest structure is consequently simplified into only canopy and evergreen shrub layers (Baker 1994, Hedman and Van Lear 1995, Baker and Van Lear 1998, Vandermast and Van Lear 2002).

The reintroduction of fire in an active (as opposed to passive) adaptive management plan prescription would not only curb the general inhibitory effect on tree regeneration of the evergreen understory layer, but specifically spur the regeneration of oaks in these forests. Active adaptive management practices treat all management actions as deliberate experiments in which the most successful outcome produces both short term yields and data that will improve better long term management (Walters and Hilborn 1978).

Introducing a large scale disturbance such as fire does not come without risks, however. In fact, burning as a management prescription cannot be safely conducted in some fragmented areas such as most of the Savage River State Forest (SRSF), which contains numerous private land ‘inholdings’ (Figure 6.2). In contrast, the Martin Hill Wild Area in the Buchanan State Forest (PA) is not interrupted by private land, and represents an ideal geographic situation within which to perform an active adaptive management experiment such as the reintroduction of fire as an ecological process. The Martin Hill Wild Area is both spatially compact and has been heavily affected by gypsy moth over the past two decades, and is therefore an area suitable to test potential management interventions (Figure 6.3). Another area where this treatment might be feasible is the southern portion of Savage Mountain in SRSF. This is a relatively uninterrupted area where it has been observed that the recruitment of *A. rubrum* and *B. lenta* has increased at the expense of oak recruitment coincident with the absence of fire during the 20th century (Shumway *et al*. 2001).

The use of burning as a treatment to reduce the abundance of *K. latifolia* and allow more desirable canopy tree seedlings to regenerate has been widely examined in Southern Appalachian forests (Minkler 1941, Hooper 1969, Wahlenburg and Doolittle 1950, Waterman *et al*. 1995, Ducey *et al*. 1996, Meyer and Swank 1996, Elliott *et al*. 1999a, 1999b, Clinton and Vose 2000). A typical treatment involves allowing a cohort of canopy-replacing tree seedlings to become established before the height and density of the regrowing *K. latifolia* – which eventually returns to dominate the understory – becomes too great (Hooper 1969, Elliott *et al* 1999a). As an added advantage associated

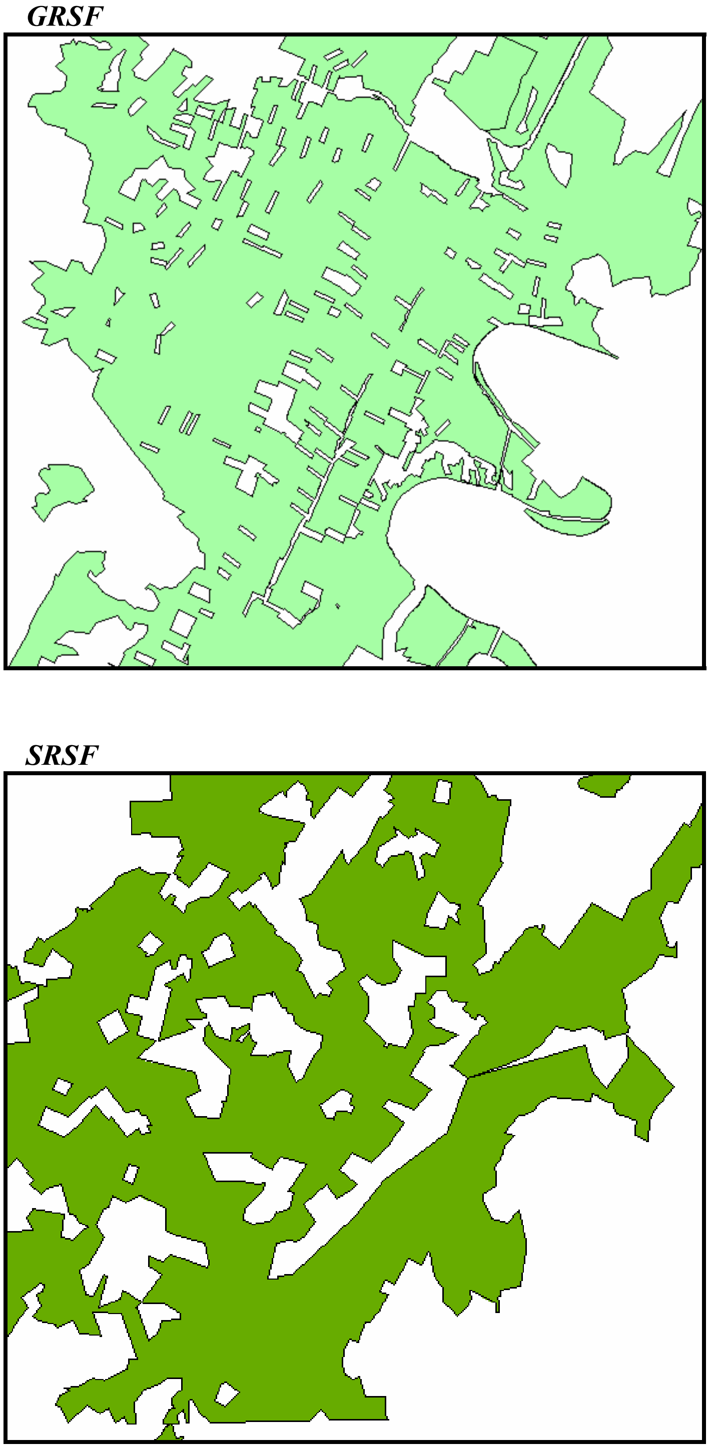


Figure 6.2: Detailed views of the ‘inholdings’ present within the extents of Green Ridge State Forest (GRSF) and Savage River State Forest (SRSF). The areas colored green are state forest land, and the non-colored portions lie outside of the state forest boundaries.

Figure 6.3: Example of an open forest canopy in the Martin Hill Wild Area of the Buchanan State Forest. This forest has experienced repeated gypsy moth infestation, which has resulted in a decrease in the amount of canopy cover and an increase in the cover of *K. latifolia* and *Q. ilicifolia* in the shrub layer.

with burning, the nutritional quality of *K. latifolia* leaves has been observed to increase in recently burned areas, providing improved forage for deer and ruffed grouse (Thackston *et al*. 1982, USDA 2002). Because deer herbivory is also cited as a contributor to oak regeneration inhibition (Abrams 2003), perhaps the enhanced forage brought about by the improved nutritional quality of *K. latifolia* leaves in recently burned areas would reduce this source of pressure on the oak seedlings re-establishing in burned areas, thus acting as a positive feedback to further augment burning as a management action.

A careful experimental design would be required to provide sufficient data to judge the effectiveness of the reintroduction of fire as an active adaptive management plan to improve the oak regeneration by reducing the inhibitory effect of the evergreen understory layer. A five to seven year period of data collection on seedling regeneration success would yield information on these two differing provinces for an adequate time period taking into consideration fluctuations in climate and pest outbreaks. Experimental treatments should include: (1) varying the seasonal timing of burning, and (2) annual sequential burns to determine which, if any, treatment yields improved oak regeneration success in areas where an evergreen understory is present and absent. It is possible that presence/absence of an evergreen understory may not control the success of seedling regeneration; rather, the simple reintroduction of fire and its overall ecosystem impacts independent of the understory layer may be sufficient to stimulate regeneration. Regardless, the beneficial effects of the evergreen understory layer in terms of forest functioning would not be imperiled by this experiment, as *K. latifolia and R. maximum* have rebounded quickly in past experiments using this treatment.

This research has shown that the evergreen understory layer dominated by *Kalmia latifolia* and *Rhododendron maximum* is an important component of the ecosystem functioning of Central Appalachian forests on the landscape scale. The evergreen understory has been shown to represent a significant physical component of central Appalachian highland forests, has been demonstrated to influence structural and nutrient dynamics, and has important feedbacks with both climatic variations and insect disturbances. This work provides a foundation to further study the overall contribution of understory shrub communities to forest community and ecosystem dynamics.

Appendix

Table A1: Ridge and Valley relative basal area, frequency of occurrence, cover, and overall rankings.

Spp	**Ranks** **RBA**	**Frequency**	**Cover**	**Overall**
Quercus prinus	1	1	1	1
Quercus rubra	2	2	2	2
Quercus alba	3	3	3	3
Quercus coccinea	4	5	5	4
Acer rubrum	8	4	7	5
Vaccinium spp	44	8	4	6
Quercus velutina	5	6	9	7
Nyssa sylvatica	7	10	10	8
Kalmia latifolia	15	14	8	9
Gaylussacia spp	36	13	6	10
Carya glabra	9	7	12	11
Hamamelis virginiana	17	12	11	12
Acer saccharinum	10	17	13	13
Pinus virginiana	6	15	15	14
Amelanchier arborea	16	11	14	15
Smilax spp	45	9	20	16
Pinus rigida	12	16	18	17
Fraxinus americana	20	21	16	18
Cornus florida	19	19	23	19
Pinus strobus	11	22	25	20
Carya tomentosa	21	18	28	21
Rhododendron maximum	14	36	17	22
Pinus pungens	13	24	26	23
Ostrya virginiana	27	23	22	24
Sassafras albidum	23	20	27	25
Vaccinium angustifolia	46	28	19	26
Prunus serotina	28	27	21	27
Liriodendron tulipifera	18	32	31	28
Carya ovata	24	25	33	29
Quercus ilicifolia	25	29	24	30
Betula alleghaniensis	22	33	29	31
Carpinus caroliniana	31	34	30	32
Cercis canadensis	33	30	32	33
Galium spp	47	26	37	34
Betula lenta	34	31	34	35
Juglans nigra	32	38	36	36
Robinia pseudoacacia	29	35	39	37
Tsuga canadensis	26	37	38	38
Lindera benzoin	48	39	35	39
Tilia americana	30	40	43	40
Magnolia acuminata	37	41	41	41
Populus tremuloides	35	42	40	42
Castanea dentata	39	43	44	43
Acer pensylvanicum	49	44	42	44
Crataegus spp	50	45	45	45
Ulmus americana	38	46	46	46
Celtis occidentalis	40	47	47	47
Pinus resinosa	41	48	48	48
Sorbus americana	42	49	49	49

Table A2: Allegheny Plateau relative basal area, frequency of occurrence, cover, and overall rankings.

Spp	**Ranks** **RBA**	**Frequency**	**Cover**	**Overall**
Quercus rubra	1	1	1	1
Acer rubrum	2	2	2	2
Quercus prinus	3	3	4	3
Kalmia latifolia	12	4	3	4
Quercus alba	4	7	7	5
Betula lenta	8	5	5	6
Nyssa sylvatica	7	8	8	7
Acer saccharinum	6	6	6	8
Tsuga canadensis	5	12	12	9
Sassafras albidum	11	9	9	10
Rhododendron maximum	9	10	10	11
Vaccinium spp	39	11	11	12
Prunus serotina	10	16	16	13
Hamamelis virginiana	19	14	14	14
Acer pensylvanicum	28	13	13	15
Fagus grandifolia	14	15	15	16
Castanea dentata	27	19	19	17
Quercus coccinea	13	23	23	18
Carya ovata	16	18	18	19
Magnolia acuminata	17	25	25	20
Fraxinus americana	20	21	21	21
Vaccinium angustifolia	40	17	17	22
Tilia americana	18	26	26	23
Liriodendron tulipifera	15	27	27	24
Quercus velutina	21	31	31	25
Amelanchier arborea	23	30	30	26
Carya glabra	22	29	29	27
Gaylussacia spp	41	20	20	28
Robinia pseudoacacia	25	33	33	29
Alliaria petiolata	42	22	22	30
Pinus strobus	26	28	28	31
Rhododendron prinophyllum	33	24	24	32
Betula alleghaniensis	24	32	32	33
Vitis spp	34	34	34	34
Ostrya virginiana	29	41	41	35
Galium spp	43	39	39	36
Crataegus spp	31	43	43	37
Prunus virginiana	44	35	35	38
Pinus rigida	30	38	38	39
Quercus ilicifolia	32	37	37	40
Cornus altinifolia	45	36	36	41
Carpinus caroliniana	35	40	40	42
Carya tomentosa	36	42	42	43
Juglans nigra	46	44	44	44
Cornus florida	37	45	45	45
Quercus palustrus	38	46	46	46

Table A3: Measurements made at the plot and subplot level at the 213 vegetation survey plots established for this research (see Figure 2.2).

Measurement Level	Observation	Method	Observations per Plot
Plot	Geographic Position	Differentially Corrected GPS	1
	Slope	Compass Declinometer	1
	Aspect	Compass	1
	Landform Type	Categorical	1
	Cover by Spp	Visual Estimate	Various
Subplot	Canopy LAI	Hemispherical Photography	12
	Visible Sky	Hemispherical Photography	12
	Shrub Layer LAI	Pin and Cord Method	12
	Stem Density	Stem Counts along Transects	2
	Basal Area	2-Factor Prism	Various
	Canopy Closure	Visual Estimate	3
	Subcanopy Closure	Visual Estimate	3
	Shrub/Sapling Cover	Visual Estimate	3
	Herb Cover	Visual Estimate	3
	Rock Cover	Visual Estimate	3
	Species Composition	2-Factor Prism	Various
	Canopy Tree Height	Laser Rangefinder	9
	Subcanopy Tree Height	Laser Rangefinder	9
	Shrub/Sapling Layer Height	Visual Estimate	Various
	Herb Layer Height	Visual Estimate	Various

Table A4: Descriptions, computations, and references for the various indices ands measures used in the classifications and ordinations performed for this research.

Name	Acronym	Computation	Reference	Description
Beers Slope Aspect Transformation	BEERS100	(cos(aspect – 45) + 1)*100	Beers *et al.* 1966	Transforms circular aspect to linear variable oriented from southwest (warm, dry) to northwest (cool, wet)
Relative Slope Position	RSP	distance to bottom/(distance to top + distance to bottom) * 100		Position on a slope face with respect to local drainage features and ridges
Topographic Convergence Index	TCI	$\ln(\alpha/\tan\beta)$ where α = slope and β = upslope contributing area	Beven and Kirkby 1979	Measure of wetness potential based on upslope contributing area and local slope angle
Terrain Shape Index	TSI	(Z')/R where Z' = mean elevation of plot and R = plot radius	McNab 1989	Identifies the local geometric shape (convex or concave) of an area based on variability of a defined space (e.g. a plot)
Land form Index	LFI	sum of slope observation / (N*100)	McNab 1993	Identifies the regional context of a location with respect to macro-topographic features, e.g. exposed ridges and protected coves
Terrain Relative Moisture Index	TRMI	slope position + curvature + slope angle + slope aspect	Parker 1982	Integrative measure of slope angle, position, aspect, and curvature scaled to represent xeric to progressively mesic and hydric conditions
Elevation in meters	ELEV			Elevations derived from digital elevation model
Gypsy Moth Infestation	GYPSY	cumulative number of years infested	A. Liebhold, pers. comm.	Gypsy moth infestation extent estimated through aerial survey
Precipitation	PPTCM	average annual precipitation between 1983 and 1998 in cm	J. Lynch, pers. comm..	Precipitation amounts in cm interpolated from gauging stations
Rock Cover	ROCKCOV			Visual estimates of rock cover percent on vegetation survey plots

Table A5: Pearson and Kendall correlations with axes derived from the NMS ordination of data from all 213 plots and the incremental and cumulative coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space.

Axis:	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
SLOPE	.299	.090	.184	.284	.081	.210	.127	.016	.080
TRMI	-.325	.106	-.218	.017	.000	-.002	.173	.030	.120
RSP	.337	.114	.217	.023	.001	-.022	-.260	.068	-.179
BEERS100	-.017	.000	.002	.139	.019	.069	.058	.003	.037
LFI	-.073	.005	-.069	.258	.067	.223	.268	.072	.166
TCI	-.416	.173	-.241	-.137	.019	-.110	.122	.015	.075
ELEV	.222	.049	.138	**-.670**	.449	-.471	.286	.082	.156
PPTCM	.161	.026	.088	**-.588**	.346	-.436	.344	.118	.224
ROCKCOV	.161	.026	.109	**-.300**	.090	-.202	**.374**	.140	.282
GYPSY	.325	.105	.205	-.095	.009	.015	**-.413**	.170	-.253

	R Squared	
Axis	Increment	Cumulative
1	.192	.192
2	.236	.429
3	.393	.821

Table A6: Pearson and Kendall correlations with axes derived from the NMS ordination of data from the 108 Ridge and Valley plots and the incremental and cumulative coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space.

Axis:	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
SLOPE	.079	.006	.090	.149	.022	.153	-.084	.007	.003
TRMI	.197	.039	.131	.321	.103	.234	.112	.013	.062
RSP	-.179	.032	-.135	-.386	.149	-.239	.072	.005	.014
BEERS100	.142	.020	.107	.176	.031	.144	.208	.043	.113
LFI	.097	.009	.067	.383	.147	.282	-.026	.001	.021
TCI	.110	.012	.034	.280	.078	.145	-.067	.004	-.031
ELEV	-.364	.133	-.229	-.436	.190	-.238	**-.624**	.389	-.450
PPTCM	-.084	.007	-.125	-.071	.005	-.050	**-.488**	.238	-.308
ROCKCOV	-.043	.002	.016	.062	.004	.066	**-.489**	.239	-.240
GYPSY	**-.566**	.321	-.431	-.428	.183	-.268	-.422	.178	-.324

	R Squared	
Axis	Increment	Cumulative
1	.236	.236
2	.356	.592
3	.206	.798

Table A7: Pearson and Kendall correlations with axes derived from the NMS ordination of data from the 105 Allegheny Plateau plots and the incremental and cumulative coefficients of determination for the correlations between ordination distances and distances in the original n-dimensional space.

Axis:	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
SLOPE	**.384**	.126	.248	.183	.033	.106	.291	.084	.132
TRMI	-.299	.090	-.145	.148	.022	.134	.036	.001	-.033
RSP	.354	.148	.232	-.239	.057	-.199	-.077	.006	-.046
BEERS100	.137	.019	.111	.024	.001	.008	.091	.008	.028
LFI	-.053	.003	-.072	**.439**	.193	.306	.340	.116	.159
TCI	**-.421**	.177	-.244	.114	.013	.061	-.082	.007	-.097
ELEV	.132	.018	.119	**-.458**	.210	-.319	-.252	.064	-.099
PPTCM	-.091	.008	-.044	-.271	.074	-.234	-.181	.033	-.092
ROCKCOV	-.048	.002	-.065	-.059	.003	-.123	.279	.078	.238
GYPSY	-.124	.015	-.084	-.090	.008	-.065	.190	.036	.144

	R Squared	
Axis	Increment	Cumulative
1	.260	.260
2	.270	.531
3	.312	.843

Table A8: Classification of evergreen understory plots in the NLCD classification in (a) the Allegheny Plateau, and (b) the Ridge and Valley study areas.

(a) Allegheny Plateau (Overall accuracy = 47%)

NLCD Classification	**Evergreen Understory Cover**			
	>75%	50-75%	30-50%	<30%
Deciduous	21%	30%	72%	91%
Mixed	54%	59%	24%	9%
Evergreen	25%	11%	3%	--

(b) Ridge and Valley (Overall accuracy = 56%)

NLCD Classification	**Evergreen Understory Cover**			
	>75%	50-75%	30-50%	<30%
Deciduous	--	50%	68%	75%
Mixed	40%	43%	28%	25%
Evergreen	60%	7%	4%	--

Table A9: Model parameters applied to cos-i correction of 2000 Landsat ETM images for the Ridge and Valley (n=297) and Allegheny Plateau (n=716) study areas. Normalization equation takes the form of Y = old TM radiance – cosi*slope – intercept + mean where Y is the new ETM radiance and the mean radiance is reported as a digital number (DN).

Parameter	**Enhanced Thematic Mapper (ETM) Bands**					
	ETM1	**ETM2**	**ETM3**	**ETM4**	**ETM5**	**ETM6**
			Ridge and Valley			
Mean (DN)	68.56	51.64	57.7	55.26	97.47	62.62
R^2	.7223	.8056	.7211	.8728	.8316	.7688
Intercept	30.045	-5.543	-48.351	-51.868	-176.22	-114.106
Slope	.231	.343	.636	.642	1.641	1.06
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
			Allegheny Plateau			
Mean (DN)	72.31	55.76	65.23	56.67	113.27	76.17
R^2	.7406	.8431	.841	.7928	.875	.8497
Intercept	27.958	-11.747	-65.031	-45.893	-198.653	-135.971
Slope	.255	.389	.750	.591	1.796	1.222
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001

Table A10: Image variables used in the classifications performed for the two study areas. Topographic variables are listed above in Table A4.

	Study Area	
Variable Type	**Ridge and Valley**	**Allegheny Plateau**
Optical	ETM1 (0.45 – 0.90 μm)	ETM1 (0.45 – 0.90 μm)
	ETM2 (0.53 – 0.61 μm)	ETM2 (0.53 – 0.61 μm)
	ETM3 (0.63 – 0.69 μm)	ETM3 (0.63 – 0.69 μm)
	ETM4 (0.75 – 0.90 μm)	ETM4 (0.75 – 0.90 μm)
	ETM5 (1.55 – 1.75 μm)	ETM5 (1.55 – 1.75 μm)
	ETM6 (2.09 – 2.35 μm)	ETM6 (2.09 – 2.35 μm)
	Principle Component 1 (PC1)	Principle Component 1 (PC1)
	Principle Component 2 (PC2)	Principle Component 2 (PC2)
	Principle Component 3 (PC3)	Principle Component 3 (PC3)
	Tasseled Cap Brightness	Tasseled Cap Brightness
	Tasseled Cap Greenness	Tasseled Cap Greenness
	Tasseled Cap Wetness	Tasseled Cap Wetness
	Soil-Adjusted Vegetation Index (SAVI)	Soil-Adjusted Vegetation Index (SAVI)
	Normalized Difference Vegetation Index (NDVI)	Normalized Difference Vegetation Index (NDVI)
SAR	Radarsat (02-18-00)	ERS (11-07-97)
	Radarsat (02-18-00) despeckled	ERS (11-07-97) texture
	Radarsat (02-18-00) texture	Radarsat (merged) PC1
		Radarsat (merged) PC2
		Radarsat (03-04-00)
		Radarsat (02-18-00) texture

Table A11: Classification schemes for the two study areas and available validation points.

Study Area	Vegetation Type	Number of Validation Plots
Ridge and Valley	Klat-dominated Understory	43
	Rmax-dominated Understory	4
N = 85	Conifer Canopy	8
	Mixed Conifer-Deciduous Canopy	10
	Understory White Pine	2
	Control (Deciduous Canopy w/ no evergreen understory)	18
Allegheny Plateau	Klat-dominated Understory	67
	Rmax-dominated Understory	9
	Mixed Evergreen Understory	12
N = 140	Hemlock Canopy	7
	Understory Hemlock	8
	Control (Deciduous Canopy w/ no evergreen understory)	37

Table A12: Frequency of classification input variable usage in decision classification trees created for both study areas.

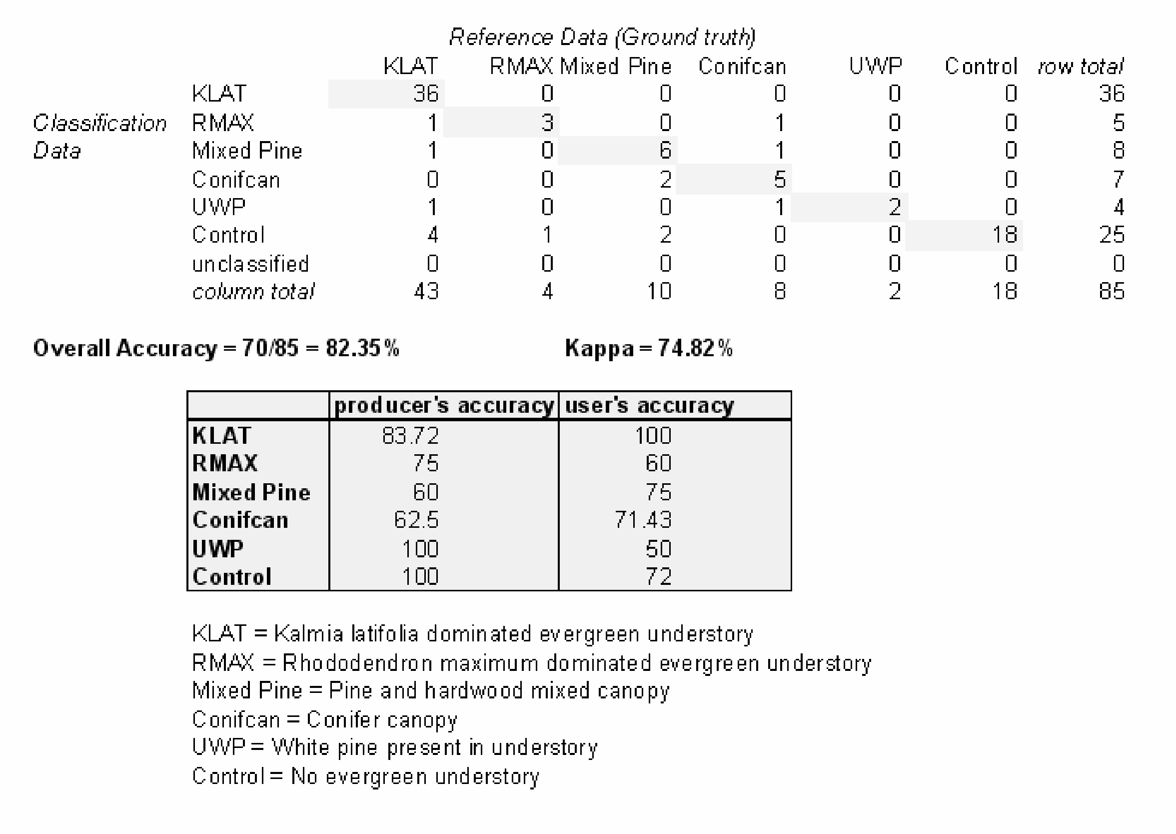
Variable	Ridge and Valley	Allegheny Plateau	Total
ETM1		2	2
ETM2		2	2
ETM3		2	2
ETM4	2	2	4
ETM5	1	5	6
PC2	3	1	4
Brightness	2	1	3
Greenness	3		3
Wetness		1	1
LFI	1	3	4
TCI		1	1
BEERS		3	3
NDVI		2	2
SAVI	1	1	2
Radarsat texture		1	1
Total	**13**	**27**	**40**

Table A13: Overall accuracy and Kappa statistics obtained from the different classification methods tested.

	Ridge and Valley		Allegheny Plateau	
Classification Method	**Overall Accuracy**	**Kappa**	**Overall Accuracy**	**Kappa**
MaxLike Optical	**87.06**	**.8063**	69.29	.2899
MinDist Optical	70.58	.5709	52.14	.3477
MaxLike Optical + Topo	87.06	.8068	80.00	.7037
MinDist Optical + Topo	50.59	.345	49.29	.2701
MaxLike Optical + Topo + SAR	84.71	.7723	71.43	.5468
MinDist Optical + Topo + SAR	72.94	.6005	61.43	.4558
ClassTree Optical	78.82	.6765	69.29	.5181
ClassTree Optical + Topo	80.00	.6934	70.71	.5785
ClassTree Optical + Topo + SAR	NA	NA	70.00	.5652
Merged MaxLike Optical + Topo	NA	NA	**82.86**	**.755**

Table A14a: Ridge and Valley maximum likelihood classification (optical and topographic data) error matrices and accuracy assessment results for (a) all classes and (b) with conifer classed combined.

(a)



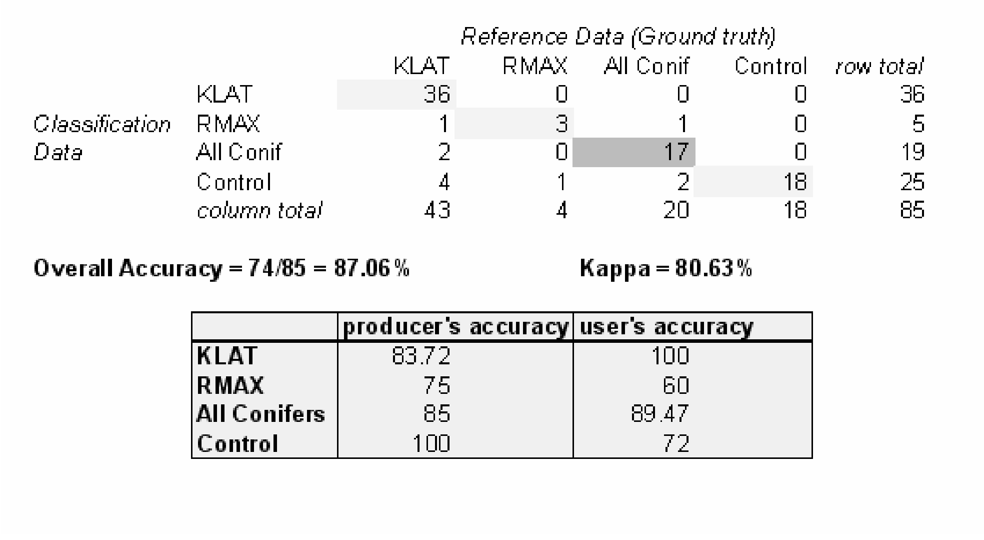
		Reference Data (Ground truth)						
		KLAT	RMAX	Mixed Pine	Conifcan	UWP	Control	*row total*
	KLAT	36	0	0	0	0	0	36
Classification	RMAX	1	3	0	1	0	0	5
Data	Mixed Pine	1	0	6	1	0	0	8
	Conifcan	0	0	2	5	0	0	7
	UWP	1	0	0	1	2	0	4
	Control	4	1	2	0	0	18	25
	unclassified	0	0	0	0	0	0	0
	column total	43	4	10	8	2	18	85

Overall Accuracy = 70/85 = 82.35% **Kappa = 74.82%**

	producer's accuracy	user's accuracy
KLAT	83.72	100
RMAX	75	60
Mixed Pine	60	75
Conifcan	62.5	71.43
UWP	100	50
Control	100	72

KLAT = Kalmia latifolia dominated evergreen understory
RMAX = Rhododendron maximum dominated evergreen understory
Mixed Pine = Pine and hardwood mixed canopy
Conifcan = Conifer canopy
UWP = White pine present in understory
Control = No evergreen understory

(b)

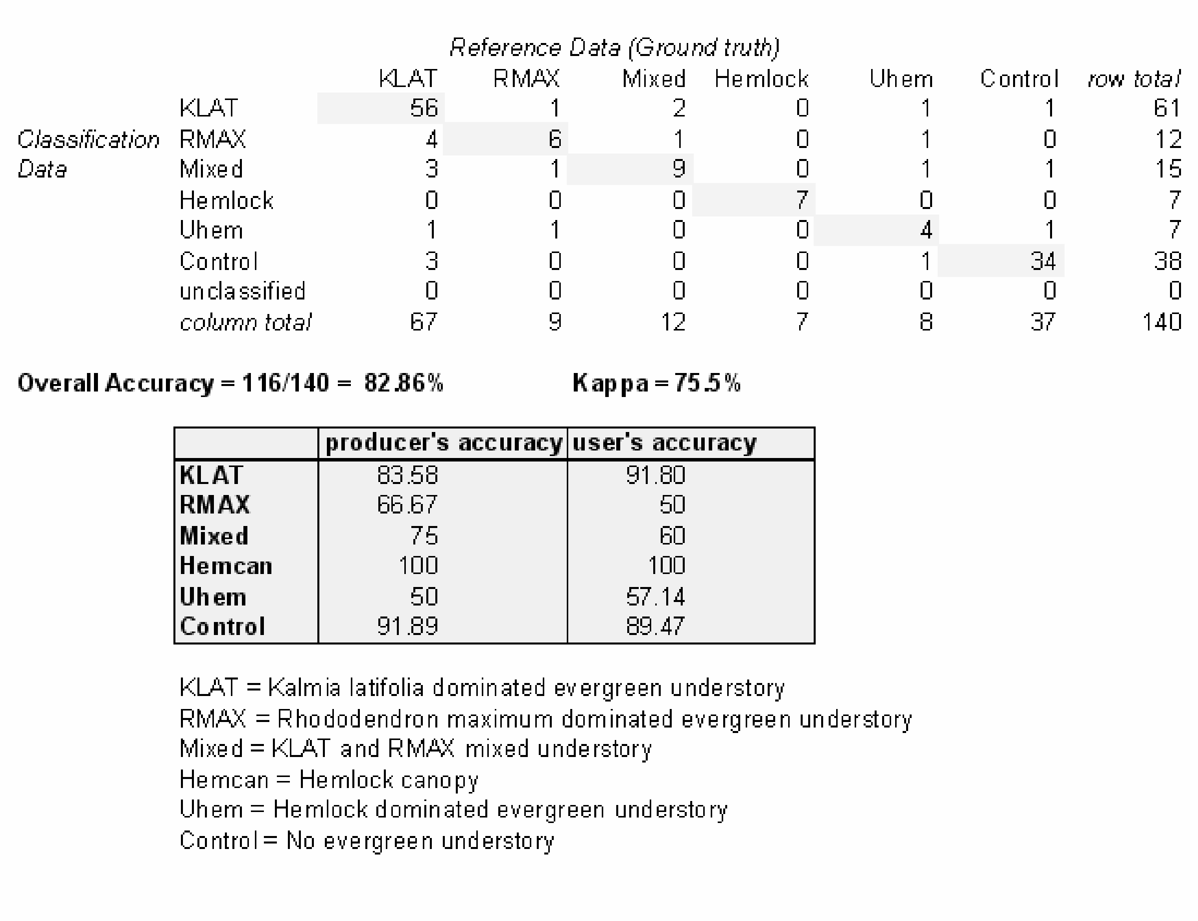


		Reference Data (Ground truth)				
		KLAT	RMAX	All Conif	Control	*row total*
	KLAT	36	0	0	0	36
Classification	RMAX	1	3	1	0	5
Data	All Conif	2	0	17	0	19
	Control	4	1	2	18	25
	column total	43	4	20	18	85

Overall Accuracy = 74/85 = 87.06% **Kappa = 80.63%**

	producer's accuracy	user's accuracy
KLAT	83.72	100
RMAX	75	60
All Conifers	85	89.47
Control	100	72

Table A15: Allegheny Plateau merged maximum likelihood and decision tree classification (optical and topographic data) error matrix and accuracy assessment results.



		Reference Data (Ground truth)						
		KLAT	RMAX	Mixed	Hemlock	Uhem	Control	*row total*
	KLAT	56	1	2	0	1	1	61
Classification	RMAX	4	6	1	0	1	0	12
Data	Mixed	3	1	9	0	1	1	15
	Hemlock	0	0	0	7	0	0	7
	Uhem	1	1	0	0	4	1	7
	Control	3	0	0	0	1	34	38
	unclassified	0	0	0	0	0	0	0
	column total	67	9	12	7	8	37	140

Overall Accuracy = 116/140 = 82.86% **Kappa = 75.5%**

	producer's accuracy	**user's accuracy**
KLAT	83.58	91.80
RMAX	66.67	50
Mixed	75	60
Hemcan	100	100
Uhem	50	57.14
Control	91.89	89.47

KLAT = Kalmia latifolia dominated evergreen understory
RMAX = Rhododendron maximum dominated evergreen understory
Mixed = KLAT and RMAX mixed understory
Hemcan = Hemlock canopy
Uhem = Hemlock dominated evergreen understory
Control = No evergreen understory

Table A16: Areal coverage of land cover categories and percent of forested portions of study areas covered by these categories.

Study Area	**Class**	**Area (ha)**	**Percent of Total Forested Area**
Ridge and Valley	KLAT	5881.6	5.86
	RMAX	246	.25
	Total Evergreen Understory	6126.6	**6.11**
	Conifer Canopy	8818.2	8.79
	Mixed Conifer	17076.2	17.02
	Understory White Pine	1943.6	1.94
	No Evergreen Understory	66337.1	66.14
Allegheny Plateau	KLAT	16104.9	15.03
	RMAX	7395.8	6.9
	Mixed	5022.7	4.69
	Total Evergreen Understory	28523.5	**26.63**
	Hemlock/Conifer Canopy	3409.9	3.18
	Hemlock Component	3847.7	3.59
	No Evergreen Understory	71331.8	66.6

Table A17. Numbers of ground control points and resulting root mean square error (RMSE) values used to georeference the time series of image data used for change detection.

Image Date	**Area Covered**	**Number of GCPs**	**RMSE**
April 12 1984	Plateau and Ridge and Valley	120	.486
March 26, 1986	Allegheny Plateau	34	.654
April 16, 1991	Allegheny Plateau	31	.449
March 1, 1992	Ridge and Valley	30	.532
April 16, 1997	Plateau and Ridge and Valley	53	.543
March 31, 2000	Plateau and Ridge and Valley	52	.568

Table A18: Model parameters applied to cos-i correction of the five Landsat TM and ETM (2000) images for the Allegheny Plateau study area. Normalization equation takes the form of Y = old TM (ETM) radiance – cosi*slope – intercept + mean where Y is the new TM (ETM) radiance.

Parameter	**Landsat TM and ETM Bands**					
	ETM1	**ETM2**	**ETM3**	**ETM4**	**ETM5**	**ETM6**
Allegheny Plateau Study Area						
Path 16 Row 33 March 31, 2000 Landsat ETM Image (n = 716)						
Mean	72.31	55.76	65.23	56.67	113.27	76.17
R^2	.7406	.8431	.841	.7928	.875	.8497
Intercept	27.958	-11.747	-65.031	-45.893	-198.653	-135.971
Slope	.255	.389	.75	.591	1.796	1.222
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 16 Row 32 April 16, 1997 Landsat TM Image (n = 1011)						
Mean	83.72	32.36	43.84	57.62	115.21	55.37
R^2	.7224	.7828	.7989	.8145	.8415	.824
Intercept	30.796	-8.272	-43.167	-42.379	-195.558	-107.97
Slope	.304	.234	.5	.575	1.786	.939
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 16 Row 33 April 16, 1991 Landsat TM Image (n = 843)						
Mean	83.01	33.33	43.19	56.65	103.68	48.12
R^2	.7543	.7947	.846	.8372	.8961	.8798
Intercept	38.93	-1.124	-35.971	-41.327	-182.533	-94.55
Slope	.253	.198	.454	.562	1.641	.818
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 17 Row 32 March 24, 1986 Landsat TM Image (n = 796)						
Mean	74.46	29.5	37.57	47.5	95.88	44.73
R^2	.8087	.8584	.8707	.86	.8961	.8852
Intercept	33.499	-3.96	-34.47	-51.041	-191.765	-99.752
Slope	.248	.202	.435	.596	1.738	.873
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 16 Row 33 April 12, 1984 Landsat TM Image (n = 611)						
Mean	92.19	38.05	49.39	61.74	116.31	115.64
R^2	.375	.6681	.8138	.8114	.8884	.5031
Intercept	55.817	5.173	-24.638	-33.918	-163.153	62.406
Slope	.211	.191	.43	.555	1.622	.309
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001

Table A19: Model parameters applied to cos-i correction of the four Landsat TM and ETM (2000) images for the Ridge and Valley study area. Normalization equation takes the form of Y = old TM radiance – cosi*slope – intercept + mean where Y is the new ETM radiance.

Parameter	**Landsat TM and ETM Bands**					
	ETM1	**ETM2**	**ETM3**	**ETM4**	**ETM5**	**ETM6**
Ridge and Valley Study Area						
Path 16 Row 33 March 31, 2000 Landsat ETM Image (n = 293)						
Mean	68.56	51.64	57.7	55.26	97.47	62.62
R^2	.7223	.8056	.7211	.8728	.8316	.7688
Intercept	30.045	-5.543	-48.351	-51.868	-176.22	-114.106
Slope	.231	.343	.636	.642	1.641	1.06
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 16 Row 32 April 16, 1997 Landsat TM Image (n = 392)						
Mean	80.85	30.91	40.88	57.61	105.97	48.92
R^2	.6794	.7207	.7207	.8463	.8508	.782
Intercept	39.206	-1.33	-28.194	-41.69	-175.12	-89.961
Slope	.244	.189	.405	.582	1.649	.815
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 16 Row 32 March 1, 1992 Landsat TM Image (n = 885)						
Mean	56.62	23	26.31	37.52	62.94	29.45
R^2	.7745	.8499	.8753	.8649	.8994	.8905
Intercept	29.738	.935	-19.884	-40.533	-138.257	-68.801
Slope	.171	.14	.294	.496	1.279	.625
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001
Path 16 Row 33 April 12, 1984 Landsat TM Image (n = 398)						
Mean	85.56	34.48	44.4	58.74	107.25	120.9
R^2	.7117	.7921	.7825	.8199	.8642	.7595
Intercept	39.508	-1.95	-31.864	-47.684	-181.8	65.179
Slope	.273	.216	.452	.631	1.713	.33
p	>.0001	>.0001	>.0001	>.0001	>.0001	>.0001

Table A20: Allegheny Plateau study area image normalization parameters. The *x* in the equations represents the radiance value of the image band being normalized.

Image Date	Band	Equation	R^2
April 12, 1984 (n = 279)	TM1	1.035x – 31.097	.7285
	TM2	1.9394x – 30.1245	.7794
	TM3	1.7431x – 32.5521	.8691
	TM4	1.1032x – 5.8622	.931
	TM5	1.0815x – 3.6347	.9216
	TM6	2.7947x – 243.2537	.6435
March 26, 1986 (n = 690)	TM1	1.1641x – 22.9228	.7648
	TM2	2.0441x – 14.7615	.8393
	TM3	1.6264x – 7.6194	.8939
	TM4	1.0655x + .4778	.9745
	TM5	.9601x + 1.695	.9713
	TM6	1.2279x + 4.7848	.9655
April 16, 1991 (n = 797)	TM1	1.064x – 21.2371	.874
	TM2	1.8262x – 9.5887	.9126
	TM3	1.5324x – 4.6429	.9448
	TM4	.819x + 1.8991	.9853
	TM5	1.0231x + 4.9393	.9859
	TM6	1.4593x + 6.5536	.9708
April 16, 1997 (n = 214)	TM1	.856x + .7777	.7862
	TM2	1.6059x + 4.6633	.834
	TM3	1.4161x + 2.7358	.8759
	TM4	.7778x + 3.9755	.9744
	TM5	.9355x + 5.9504	.9853
	TM6	1.3191x + 7.1287	.9846

Table A21: Ridge and Valley study area image normalization parameters. The *x* in the equations represents the radiance value of the image band being normalized.

Image Date	**Band**	**Equation**	**R^2**
April 12, 1984 (n = 400)	TM1	.8505x – 8.316	.6638
	TM2	1.5912x – 10.6944	.7002
	TM3	1.3132x – 4.8956	.8419
	TM4	.9403x – 1.7528	.9664
	TM5	.9051x + .6659	.9658
	TM6	3.3041x – 333.4614	.9684
March 1, 1992 (n = 583)	TM1	1.8884x + 18.346	.8786
	TM2	2.2049x + 14.1599	.9323
	TM3	2.2174x + .8664	.9655
	TM4	1.0821x + 4.0551	.9804
	TM5	.8496x – .3104	.9821
	TM6	.7631x + .5384	.974
April 16, 1997 (n = 393)	TM1	.7811x + 5.0397	.9375
	TM2	1.6296x – 1.3903	.9647
	TM3	1.3502x – 2.4348	.9726
	TM4	.796x + .362	.9873
	TM5	.9338x + .1764	.9887
	TM6	1.3849x + .917	.9838

Table A22. Allometric and linear regression equations used to estimate the total aboveground biomass (TAB) and leaves and bark/wood biomass from dbh (cm) for species and species groups present in the watersheds selected for this research (from Jenkins *et al*. 2003† and Monk *et al*. 1985*).

Species Group (*spp*)	**Equation**	**N**
Soft maple/birch†	TAB = Exp(-1.9123 + 2.3651*ln(dbh))	316
A. Rubrum	leaves = (Exp(-4.0813 +5.8816/dbh))*bm	632
Betula spp		
Mixed hardwood†	TAB = Exp(-2.48 + 2.4835*ln(dbh))	289
F. Americana	leaves = (Exp(-4.0813 +5.8816/dbh))*bm	632
L. tulipifera		
P. serotina		
S. albidum		
Tilia spp.		
U. americana		
Hard maple/oak/hickory/beech†	TAB = Exp(-2.0127 + 2.4342*ln(dbh))	485
A. saccharum	leaves = (Exp(-4.0813 +5.8816/dbh))*bm	632
Carya spp.		
Q. alba		
Q.coccinea		
Q. prinus		
Q.rubra		
Q. velutina		
Hemlock†	TAB = Exp(-2.5384 + 2.4814*ln(dbh))	395
T. canadensis	leaves = (Exp(-2.9584 +4.4766/dbh))*bm	777
Pine†	TAB = Exp(-2.5356 + 2.4349*ln(dbh))	331
P. pungens	leaves = (Exp(-2.9584 +4.4766/dbh))*bm	777
P. resinosa		
P. rigida		
P. strobus		
P. virginiana		
Spruce†	TAB = Exp(-2.0773 + 2.3323*ln(dbh))	212
Picea spp.	leaves = (Exp(-2.9584 +4.4766/dbh))*bm	777
Apen/alder/cottonwood/willow†	TAB = Exp(-2.2094 + 2.3867*ln(dbh))	230
Populus spp.	leaves = (Exp(-4.0813 +5.8816/dbh))*bm	632
K. latifolia* leaves	leaves = 17.23 + 32.14*(dbh)	45
K. latifolia* bark and wood	bark/wood = 74.92 + 842.27*(dbh)	45
R. maximum* leaves	leaves = -886.98 +422.15*(dbh)	45
R. maximum* bark and wood	bark/wood = -9709 + 3274.44*(dbh)	45

Table A23. Ranking in abundance of aboveground and leaf biomass for *K. latifolia* and *R. maximum* among all species for each of the seven watersheds selected for this research.

Watershed	***K. latifolia* Biomass**		***R. maximum* Biomass**		**Total N Species**
	Aboveground	**Leaf**	**Aboveground**	**Leaf**	
Ridge and Valley					
Bear Gap Run	6	6	15	13	15
Laurel Branch	10	8	13	7	15
Wildcat Run	8	6	15	13	15
Allegheny Plateau					
Big Run	17	13	16	7	27
Bluelick Run	17	14	14	4	25
Monroe Run	15	15	17	7	22
Poplar Lick	20	15	18	5	25

List of Abbreviations

BA	Basal area
BEERS	Beers slope aspect transformation
BSF	Buchanan State Forest
CFI	Continuous forest inventory
DEM	Digital elevation model
Elev	Elevation measured in meters
ETM	Enhanced thematic mapper
GIS	Geographic information system
GRSF	Green Ridge State Forest
KLAT	*Kalmia latifolia*
LAI	Leaf area index
LFI	Land form index
N	Nitrogen
NDVI	Normalized difference vegetation index
NMS	Nonmetric multidimensional scaling
PDSI	Palmer drought severity index
PC1	Principal component 1
PC2	Principal component 2
PC3	Principal component 3
Pptcm	Precipitation measured in centimeters
RBA	Relative basal area
RMAX	*Rhododendron maximum*
Rockcov	Percent rock cover
RSP	Relative slope index
SAVI	Soil-adjusted vegetation index
SRSF	Savage River State Forest
TM	Thematic mapper
TRMI	Terrain relative moisture index
TCI	Topographic convergence index
TSI	Terrain shape index

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