This is to certify that the

thesis entitled
HABITAT QUALITY AND UTILIZATION ANALYSIS IN A SPATIAL
CONTEXT: THE CASE OF LUPINUS PERENNIS L. AND LYCAEIDES
MELISSA SAMUELIS NABOKOV, (LEPIDOPTERA: LYCAENIDAE)

presented by

Lisa Michelle Greenfeld

has been accepted towards fulfillment
of the requirements for

Masters degree in **Forestry**

Major professor

Date 19 September 1997

PLACE IN RETURN BOX
to remove this checkout from your record.
TO AVOID FINES return on or before date due.

DATE DUE	DATE DUE	DATE DUE
OCT 1 2 1999	MAR 1 6 2004 051004	112106
MAY 1 5 2000 6353	NOV [illegible] 2007	
FEB 2 5 2006 082406		
NOV 0 9 2006		

1/98 c:/CIRC/DateDue.p65-p.14

HABITAT QUALITY AND UTILIZATION ANALYSIS IN A SPATIAL CONTEXT: THE CASE OF *LUPINUS PERENNIS* L. AND *LYCAEIDES MELISSA SAMUELIS* NABOKOV, (LEPIDOPTERA: LYCAENIDAE)

By

Lisa Michelle Greenfeld

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTERS OF SCIENCE

Department of Forestry

1997

ABSTRACT

HABITAT QUALITY AND UTILIZATION ANALYSIS IN A SPATIAL CONTEXT: THE CASE OF *LUPINUS PERENNIS* L. AND *LYCAEIDES MELISSA SAMUELIS* NABOKOV, (LEPIDOPTERA: LYCAENIDAE)

By

Lisa Michelle Greenfeld

The first objective of this research was to evaluate tree-moderated environmental variables that affect lupine growth and density: light and soil pH, via a field study and a controlled greenhouse study. My results indicated that a pH range of 4.2 to 5.6 and 100% light provide the best conditions for lupine growth. However, because of the potential for weather extremes, land managers protecting Karner blue butterfly (KBB) sites should aim to provide lupine within a range of light levels by adjusting canopy cover.

The second objective of this study was to assess how KBB and lupine distribution are affected by spatial parameters and landscape level forest characteristics via an exploratory analysis of stand data, and lupine and KBB distribution. Patches where lupine and KBB were present tended to be in medium density stands, closer to one another, more complex, and larger, than lupine areas where KBB was absent. Patches where lupine was present were more likely to be in the low stand density class and less likely to be in the high density class than areas where lupine was absent.

To Chuck, with all of my love.

Acknowledgments

This research was funded by the McIntire-Stennis competitive grant, MSU MAWGAP fellowship and the MSU Department of Forestry.

I would like to thank the many people who helped to make this project a success. I could not have done it without my committee: Dr. Jeremy Fried, Dr. Deb McCullough, and Dr. Robert Haack. I appreciated their time, patience, helpfulness, suggestions, and ideas.

Many others provided valuable assistance to this study. Dr. Phu Nguyen provided lab space, ecology and chemistry knowledge; Dr. Don Dickmann provided flight time and the first review of my first proposal; Dr. Carl Ramm provided hours of statistical advice and expertise; Dr. Rich Kobe helped me with his ecological insights and statistical suggestions; Dr. Dan Brown provide assistance with FRAGSTATS and GIS questions; Mary Rabe and Cathy Papp Herms were very generous in sharing their Karner blue data with me; Dr. John Biernbaum, Dr. Art Cameron, Randy Klevickas, Paul Bloese, Dr. Royal Heins, Dr. Boyd Ellis, and Dr. Bruno Reissmam were very helpful with my greenhouse study; Maria Albright and John Lerg at ASGA provided data, guidance, assistance, and much friendliness during my field work; Dr. Sam Chan and Dr. Andy Gray generously allowed me to use their photo analyzing equipment, both in the field and in their lab; the secretarial staff was very helpful with the many details. I'd like to express my sincere gratitude to all of these individuals.

I would also like to thank the many friends that were supportive in times of stress, fun, and hard work and that went above and beyond the call of helpfulness during my project (e.g. watering plants, standing out in the freezing cold with the GPS, helping me make maps, re-teaching me statistics, shoveling soil, sifting soil,…). You helped me to learn a lot about forestry, relationships, and myself. Thanks to Sarah Synowiec, Sean Canavan, Demetris Gatziolis, Mark Zweifler, Greg Winter, Dave Neumann, Georgia Peterson, Gem Castillo, Andy David, Peggy Payne, Joe Zeleznik, and Steve and Jan Michmerhuizen.

Finally, I would like to thank my family for all of their support through out my education. I sincerely appreciate my mother's encouragement, love, and wisdom and my sisters' patience and support, and Chuck's love, understanding, help, and listening abilities, without which I would not have made it through the last three years!

TABLE OF CONTENTS

List of Tables viii

List of Figures ix

Chapter 1
General Introduction 1
  Introduction and Literature Review 2

Chapter 2
The Effect of Light and Soil pH on *Lupinus Perennis* Growth and Density in Michigan Oak Savanna Forest Stands 6
  Abstract 7
  Introduction 8
  Methods 10
    Field study 11
      Study Area 11
      Sampling 11
      Data Analysis 15
    Greenhouse study 16
      Methods 16
      Data Analysis 17
  Results 18
    Field Study 18
    Greenhouse Study 23
  Discussion 25
  Conclusions 28
  Bibliography 29

Chapter 3
The Effect of Landscape Level Spatial Parameters and Forest Structure on the Distribution of *Lupinus Perennis* and *Lycaeides melissa samuelis* Nabokov. 32
  Abstract..........33
  Introduction..........34
  Methods..........40
    Data processing and analysis..........40
  Results..........48
  Discussion..........52
  Conclusions..........53
  Bibliography..........55

Overall Conclusions..........59

Appendix A..........61

Appendix B..........62

Bibliography..........63

LIST OF TABLES

Table 1 - Area, perimeter, and number of plots at the six study sites.....................12

Table 2 - Regression model statistics for each iteration of the factor-ceiling distributions partitioned regression for proportion of direct light vs. lupine stem density (number/5 m^2)...20

Table 3 - Effects of light on *Lupinus perennis* biomass when grown in a greenhouse for 115 days; N = 41 24

Table 4 - Geographic information system (GIS) coverages and associated attributes used to analyze landscape properties and their relationship to KBB and lupine habitat at Allegan State Game Area, Allegan Michigan, 1995 42

Table 5 - Class level pairwise comparisons of spatial statistical output from FRAGSTATS for areas with lupine absent (LA), lupine present (LP), lupine present and KBB absent (LPKA), and lupine and KBB both present (LPKP)..49

LIST OF FIGURES

Figure 1 - Map of study sites at Allegan State Game Area (ASGA), Allegan, Michigan, May 1995..13

Figure 2 - Scatterplot of lupine density on soil pH at Allegan State Game Area, MI, 1995...18

Figure 3 - Scatterplot of stem density on proportion of direct light at Allegan State Game Area (ASGA), June-July 1995; "predicted" refers to the regression: stem density = 0.5007 (proportion of direct light) + 5.4351 (N = 443; adjusted r squared = 0.102).......................................21

Figure 4 - Scatterplot of stem density on proportion of direct light at Allegan State Game Area (ASGA), June-July 1995; "predicted" refers to the fitted frontier regression: stem density =1.6085 (proportion of direct light) + 96.538; (N = 20; adjusted r squared = 0.739)..21

Figure 5 - Histograms of the number of plots by proportion of direct light for four lupine foliar desiccation classes: a) green; b) mostly green; c) mostly brown; d) brown...22

Figure 6 - Map of areas with lupine present, KBB present (LPKP); areas with lupine present, KBB absent (LPKA), and areas with lupine absent, KBB absent (LAKA) at Allegan State Game Area (ASGA), Allegan, MI 1995..23

Figure 7 - Frequency of stands by density class for the qualifiers: all stands (AS), lupine absent (LA), lupine present (LP), lupine present, KBB absent (LPKA), and lupine present, KBB present (LPKP) at Allegan State Game Area, Allegan, MI, 1995.............................51

Figure 8 - Frequency of stands by size class for the qualifiers all stands (AS), lupine absent (LA), lupine present (LP), lupine present, KBB absent (LPKA), and lupine present, KBB present (LPKP) at Allegan State Game Area, Allegan, MI, 1995.......................................51

Chapter 1

General Introduction

Introduction and Literature Review

The Karner blue butterfly (KBB), *Lycaeides melissa samuelis* Nabokov, (Lepidoptera: Lycaenidae) was added to the federal endangered species list in December 1992 following a period of extensive habitat decline (Dirig, 1988; Haack, 1993). To protect this species, it is imperative to know what site characteristics are commonly linked with healthy KBB populations. The intent of this study was to develop knowledge about KBB's habitat needs so that managers can better protect this species.

The Karner blue butterfly, first identified in 1861 by Edwards, was ultimately named by Nabokov in 1943 after Karner, New York, the collection site of the type specimen (Haack, 1993). Karner blue have historically been observed in a region stretching from New Hampshire to Minnesota, and as far south as Ohio. Today, they are known to occur in parts of New Hampshire, New York, Michigan, Indiana, Wisconsin, and Minnesota (Haack, 1993). Adults are small (2.2-3.2 cm long), purplish-blue, bivoltine (two generations per year) butterflies with orange and black spots. Eggs and larvae are green and difficult to spot when attached to vegetation (Clough, 1992; Haack, 1993; Opler and Krizek, 1984; Scudder, 1889). Larvae feed exclusively on the leguminous perennial *Lupinus perennis* L. (Haack, 1993; Smallidge and Leopold, 1992; Stuart and Ricci, 1988; WI DNR, 1993). Adults of the first generation (May-June) rely on lupine flowers for some of their nectar needs, but adults of the second generation (July-August) require other nectar sources because lupine plants are no longer in flower (Haack, 1993). Ant tending of KBB larvae appears to play an important role in larval survival (Haack, 1993). The predators and parasites which affect Karner blue include various spiders, a stink bug, robber flies, assassin bugs, a tachnid fly, a braconid wasp, and two ichneumonid wasps (Haack, 1993 and references therein).

Scientists have shown that habitat preservation is the key to species preservation (e.g., Loehle and Wein, 1994). This is particularly evident in the case of the Karner blue butterfly, a habitat specific species (Dirig, 1988). Recently, the KBB recovery team (mandated by the Endangered Species Act) have been working on a description of Karner blue habitat. In Michigan, the habitat has been described as oak savannas with an understory of lupine and other nectaring plants (Hermes, 1996; Pickering and Gebauer, 1993; Shuey, *et. al*, 1987; Welch, 1993). Because this description does not address such specifics as the amount of lupine required, the size, shape, and distribution of suitable areas, or the ecological requirements of lupine, managers still lack critical knowledge for reversing the decline of Karner blue.

To restore remnant populations of Karner blue butterflies to sustainable levels, land managers need to consider the impacts of their actions on lupine, the Karner blue's sole larval food plant (Haack, 1993; Smallidge and Leopold, 1992; Stuart and Ricci, 1988; WI DNR, 1993). A better understanding of lupine's ecological requirements is an important first step towards managing the recovery of the Karner blue.

Lupinus perennis is a member of the pea family and is the only lupine native to the eastern US (Hultman, 1978). The name "lupine", derived from lupus, was chosen because the genus was thought to "wolf up" resources (Edsall, 1985); however, this belief proved false. Lupine fixes nitrogen, which is important since it usually grows on nutrient-poor, sandy soils (Cryan and Dirig, 1978) that are well to excessively well-drained and prone to drought (Smallidge and Leopold 1992). Lupine have 7-15 oblanceolate to obovate leaflets with strong midribs and an entire margin per palmate leaf (Hultman, 1978; Miller and Whiting, 1895; Smith, 1966). Flowers ranging from white to blue in color have five petals that are approximately one cm long on short pedicles in loose terminal racemes (Miller and Whiting, 1895; Smith, 1966). Seeds, formed in brown pubescent seed pods in mid-summer, are thrown as much as 3 meters when ripe (Edsall, 1985).

Several researchers have demonstrated links between spatial patterns of understory vegetation and variations in microhabitat caused by the differential influence of individual trees on soil properties and light intensity (e.g., Crozier and Boerner, 1984; Parker and Muller, 1982; Zinke, 1962). Because *L. perennis* is rarely found in dense forests, most researchers have assumed that the species cannot survive under deep shade (Bess, 1989; Maxwell and Givnish, 1993; Pickering and Gebauer, 1993; Smallidge and Leopold 1992). However, relationships between lupine characteristics (e.g. percent cover, number of flowering stalks, number of stems) and indices of light such as percent tree and shrub cover (Pickering and Gebauer, 1993) have not been quantified.

Some have suggested that pH may have a strong influence on lupine growth (Pickering and Gebauer 1993). On alkaline soils, growth is highly variable among many lupine species and genotypes, but lupine growth is typically poor relative to soils with lower pH. The optimal pH range for *Lupinus angustifolius* growth has been estimated via controlled experiments at 5.0 to 5.5 (Tang *et al.*, 1992). No studies have yet addressed the link between soil pH and plant growth for *L. perennis.*

A better understanding of the underlying ecological factors that determine the quality of Karner blue habitat is essential to facilitate recovery efforts for the species.

This research has two foci. The first was to evaluate the effects of two tree-moderated environmental variables which affect lupine growth and density: light and soil pH. A field study and a greenhouse study were used to analyze these relationships. The second objective was to evaluate the spatial parameters that affect lupine and KBB distribution. I used a GIS and FRAGSTATS (a spatial statistics program) to answer questions about the relationships between KBB and lupine distribution and (1) landscape metrics (e.g., size, shape, edge, proximity, patch density) and (2) forest characteristics (e.g., overstory size class, and overstory density).

Chapter 2

The Effect of Light and Soil pH on *Lupinus Perennis* Growth and Density in Michigan Oak Savanna Stands.

Abstract

The Karner blue butterfly (KBB), *Lycaeides melissa samuelis* Nabokov, (Lepidoptera: Lycaenidae) was added to the federal endangered species list in December 1992 following a period of extensive habitat decline. To restore remnant populations of Karner blue to sustainable levels, land managers need to consider the impacts of their actions on lupine, the Karner blue's sole larval food source. This research focused on two tree-moderated environmental variables that affect lupine growth and density: light and soil pH. The relationships among these variables were examined in both a field study and in a controlled greenhouse study. Light and soil pH appear to affect lupine growth and density. Lupine were found almost exclusively on soils with a pH range of 4.2 to 5.6. The highest available light (100%) provides the best conditions for lupine growth. However, because of the potential for weather extremes such as early summer drought and late spring frost, land managers should aim to promote lupine by adjusting canopy cover to provide a range of light levels.

Introduction

Scientists have shown that habitat preservation and/or restoration is the key to species preservation (e.g., Loehle and Wein, 1994). However, moving from a conceptual to an operational definition of habitat for particular species is no small task. This is especially true in the case of the Karner blue butterfly, (KBB), *Lycaeides melissa samuelis* Nabokov (Lepidoptera: Lycaenidae), a species dependent on one of the most rare habitats in the northeastern US, oak savanna and pine barrens (Dirig, 1988). This species was added to the federal endangered species list in December 1992 following a period of extensive habitat decline (Dirig, 1988; Haack, 1993). Lack of an operational habitat definition for KBB has slowed recovery efforts and led to intense efforts to identify critical habitat for this species.

In Michigan, KBB populations occur primarily in oak savannas with an understory of lupine and other nectaring plants (Pickering and Gebauer, 1993; Shuey, *et. al*; 1987; Welch, 1993). Because this description does not address such specifics as the amount of lupine required, the size, shape, and distribution of suitable areas, or the ecological requirements of lupine, managers lack information that is critical for reversing the decline of Karner blue.

To restore remnant populations of Karner blue to sustainable levels, land managers need to consider the impacts of their actions on lupine, the Karner blue's sole larval food source (Haack, 1993; Smallidge and Leopold, 1992; Stuart and Ricci, 1988; WI DNR, 1993). A better understanding of lupine's ecological requirements is a critical step towards managing the recovery of KBB. *Lupinus perennis* is a member of the pea family and is the only lupine native to the eastern U.S. (Hultman, 1978). Lupine fixes nitrogen and grows on nutrient-poor, sandy soils (Cryan and Dirig, 1978) that are well to excessively well-drained and prone to drought (Smallidge and Leopold 1992).

Several researchers have demonstrated links between spatial patterns of understory vegetation and variations in microhabitat caused by the differential influence of individual trees on soil properties and light intensity (e.g., Crozier and Boerner, 1984; Parker and Muller, 1982; Zinke, 1962). Such findings suggest that the response of herbaceous plants to their environment depends on highly localized characteristics that are rarely captured by landscape or stand level averages (Clark, 1991). Tree-induced environmental variation is particularly noticeable in savannas and variation in soil properties is a frequently cited example (Bray, 1955 cited in Curtis, 1959; Holland, 1973; Parker, 1977). Trees can have major effects on many environmental factors that probably influence lupine growth, density and distribution and subsequently, KBB populations.

Because *L. perennis* is rarely found in dense forests, most researchers have assumed that it cannot survive under deep shade (Bess, 1989; Maxwell and Givnish, 1993; Pickering and Gebauer, 1993; Smallidge and Leopold 1992). Flowering has been correlated to canopy cover, reportedly reaching maximum levels in stands of intermediate canopy cover (40-60%) (Maxwell and Givnish, 1993; WI DNR, 1993). In the Albany pine bush in New York, home of one of the largest single populations of Karner blue, *L. perennis* has the greatest stem density where canopy cover is between 10 and 40%, and the greatest reproductive success under 10-30% canopy cover (Pickering and Gebauer, 1993). In another study, *L. perennis* density was observed to be low and its flowering ability impaired in open areas (0-5% canopy cover) in southern Ontario (Boyonoski, 1992). Though not entirely consistent, these results highlight the importance of light in determining the distribution of *L. perennis* (Maxwell and Givnish, 1993; Pickering and Gebauer, 1993). Managers attempting to enhance lupine will need more precise quantification of the relationships between lupine characteristics (e.g., number of flowering stalks, number of stems) and indices of light such as proportion of direct light (PDL) (Pickering and Gebauer, 1993).

Soil pH may also influence lupine growth (Pickering and Gebauer 1993). On alkaline soils, growth is highly variable among many lupine species and genotypes, but is typically poor relative to soils with lower pH. Growth variability has been attributed to variation in root growth (Tang *et al.*, 1992), shoot growth in response to iron deficiency (Cowling and Clements, 1993), and decreases in symbiotic nitrogen fixation (Tang and Robson, 1993). No studies have yet addressed the link between soil pH and plant growth for *L. perennis.* A better understanding of the underlying ecological factors that determine the quality of Karner blue habitat is essential to facilitate recovery of this species. This research focuses on two tree-moderated environmental variables that affect lupine growth and density: light and soil pH. The relationships among these variables were examined both in a field study in areas known to be occupied by KBB and in a controlled greenhouse study.

Methods

Two complementary approaches were taken to evaluate the relationships between light and lupine growth. A field study was conducted to assess environmental conditions where lupine is present. A controlled experiment in the greenhouse provided a consistency check and an opportunity to address the effects of light under controlled conditions. In the field study, the dependent variable was stem density on fixed plots; in the greenhouse study the dependent variable was growth.

Field study

Study Area

The Allegan State Game Area (ASGA) in southwest Michigan's Allegan County was selected as the location for field experiments because it is one of two major areas in Michigan where Karner blue is found today. Forests of black and white oak (*Quercus veluntia* and *Quercus alba*) cover most of the area. Soils are very well-drained and sandy; most are in the Oakville fine sand series. Attempts to farm this land early in the century failed because the sandy soils were too infertile to support crops. By the 1930's, much of this area reverted to the state when landowners failed to pay taxes (John Lerg, Forester, ASGA Pers. com., 1995).

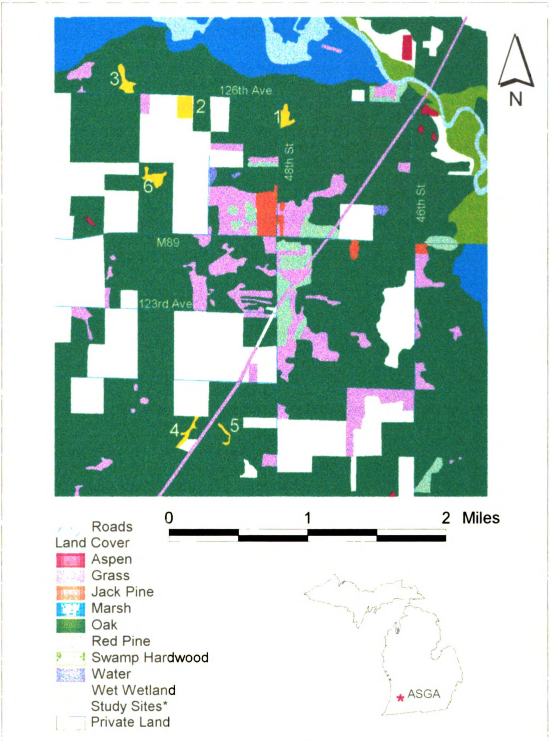
Sampling

In spring 1995, six temporary study sites were established at ASGA in open areas where Karner blue population sampling had been conducted in 1993 and 1994 (Herms, 1996). These grass/forb dominated openings within the oak forest matrix varied in shape, size, and lupine density (Table 1). At each site, plot center-points were established on a 10 by 10 meter grid spanning open areas and forest edges. There were 42 to 100 plot centers/site depending on the size of the site. Plots were positioned from a random starting point using a measuring tape and compass, and plot centers were marked with numbered flags.

Table 1. Area, perimeter, and number of plots at the six study sites.

Study sites	Area (m^2) [1]	Perimeter (m)	Number of plots
1	28,223	263	100
2	9,995	121	100
3	32,720	321	100
4	20,485	347	70
5	10,637	238	42
6	30,969	305	70
Total	133,029	1,595	482

[1] The area and perimeter of study site 2 were estimated.



*All study sites are on the grass cover type.

Figure 1. Map of study sites at Allegan State Game Area (ASGA), Allegan, Michigan, May 1995

A five m^2, temporary circular plot was established at each plot center by rotating a 1.262 m stick with one end held over the plot center. Lupine stems and flowers were counted within the plots at peak flowering, in early June.

Canopy cover was determined using hemispherical photography, a method which provides a consistent, objective index of available light (Chan *et al.*, 1986). Black and white negative film (Kodak T-max 100) was used and exposures were made with a Cannon AE-1 Program fitted with a 7.5 mm focal length proportional fisheye lens mounted on a tripod 38-51 cm above the ground. Exposure goals were: F stops ≥ 5.6, and shutter speeds of 1/125 second or faster. I used a light meter to bracket the F stop and shutter speed at each plot center. Excluding the sun from the camera's field of view is a requirement of this method, so most exposures were made near dawn or dusk when the sun was below or near the horizon. A total of 964 exposures were completed between June 27 and July 20, 1995. Proportion of direct light (PDL) at each plot center was estimated from the corresponding hemispherical photo using a software program called CANOPY (Los Alamos National Laboratory, Los Alamos, New Mexico) which utilizes an efficient image combination algorithm to categorize digitized images of the slides as PDL (Rich, 1989) (see appendix A).

One soil core of the entire A horizon was collected at each plot center with a 2 cm diameter soil corer. The samples from each plot were stored in paper bags and air dried. Each sample was then evenly mixed, and hand-processed to remove roots. Ten grams of soil were drawn from each homogenized sample and combined with 10 ml deionized water on a shaker for 30 minutes. The pH of the resulting slurry was measured using a Corning ion analyzer 250 (Corning, Corning, New York).

The early summer of 1995 was abnormally hot and dry, and lupine senescence occurred far earlier than normal (Dirig, 1973). To document this phenomenon, lupine desiccation on all plots was assessed using a subjective, ordinal scale (1 - entirely green, 2 - mostly green, 3 - mostly brown, and 4 - entirely brown).

In 1996, aerial photography was attempted with the intent of delineating all recognizable lupine patches. Unfortunately a late May frost which killed virtually all of the lupine flowers, and an extended period of cloudy weather doomed this effort. Casual on-site observations revealed intact flowers only on lupine plants growing under the protection of the forest canopy or individual trees.

Data Analysis

The relationship between soil pH and lupine density was assessed via scatterplots and correlation analysis. The relationship between light and lupine density was assessed via factor-ceiling distributions partitioned regression, an exploratory data analysis technique described by Thomson et al. (1996). Associations between light and lupine desiccation was examined via histograms and Spearman's rank correlation.

Greenhouse study

Methods

A controlled experiment was conducted to quantify effects of three light treatments, 100%, 65%, and 35% of ambient light.[1] The 35% and 65% treatments were created by stretching shade cloth with these ratings over frames constructed of electrical conduit and positioned 1 meter above the potted plants. Fifty-four, 25.4 cm deep pots were thoroughly cleaned, dried, placed in saucers, and distributed among the three treatments.

Lupine seed was collected from ripe pods at ASGA in July, 1995. Seeds were removed from pods and stored at 3 ° C in a sealed plastic bag until sowing. Seeds free of obvious deformities (e.g., wrinkled, dehydrated or underdeveloped) were scarified with a file, soaked in deionized water for 12 hours and coated with *Rhizobium lupini*. Five seeds were sown in each pot at a depth of ½ cm in soiless potting media (a mixture of peat, pearlite, and vermiculite) in February 1997[2]. After two weeks, plants were thinned to one plant per pot. Attempts were made to transplant excess seedlings into pots in which no seedlings had emerged, but these were largely unsuccessful.

Media moisture in the pots was maintained (40-70% saturated by weight) via subirrigation using well water with a fertilizer treatment of 20-2-20 NPK. Plants were

---

[1] This experiment was conducted in a temperature controlled greenhouse at Michigan State University, East Lansing Michigan from February - June, 1997 in which ambient light was augmented with 110 watt fluorescent lamps daily between pm and 1:10 am)

[2] A previous attempt (from April to September 1996) to conduct this experiment, which also included pH as a manipulated variable, was aborted due to high mortality of lupine unrelated to specific light and pH treatment. In the course of this experiment, I learned that pH could not be manipulated without undesirable impacts on plant nutrition.

treated with fungicides monthly and sprayed for insect and other fungal problems as needed. Appendix B contains a complete log of all treatments.

All plants were harvested in mid-June 1997, 115 days after planting. Roots were separated from above-ground plant material and stored in paper bags. Leaves were weighed and assessed for leaf area using a leaf area meter (Decagon Devices, Inc. Delta-T Area Measurement System. Pullman, WA, USA). Leaves and roots were dried at 21 ° C for 24 hours, then weighed. Any remaining potting media was removed from roots prior to weighing.

Data Analysis

The relationship between light and growth was tested via the Kruskal-Wallis t-sample test, a nonparametric rank-based test designed to handle non-normally distributed data which is appropriate for small sample sizes (less than 30).

Results

Field Study

Although no statistically significant (p=.05) linear relationship between soil pH and lupine density was identified via regression analysis (adjusted r squared = .039), a scatterplot of this relationship for all plots on all sites suggests that lupine at ASGA was restricted to soils with pH between 4.2 and 5.6[3] (Figure 2). Results among the six individual sites were similar. The mean soil pH for plots with lupine stems present was 4.85 (sd ± 0.30); for plots without lupine stems, the mean was 4.70 (sd ± 0.43).

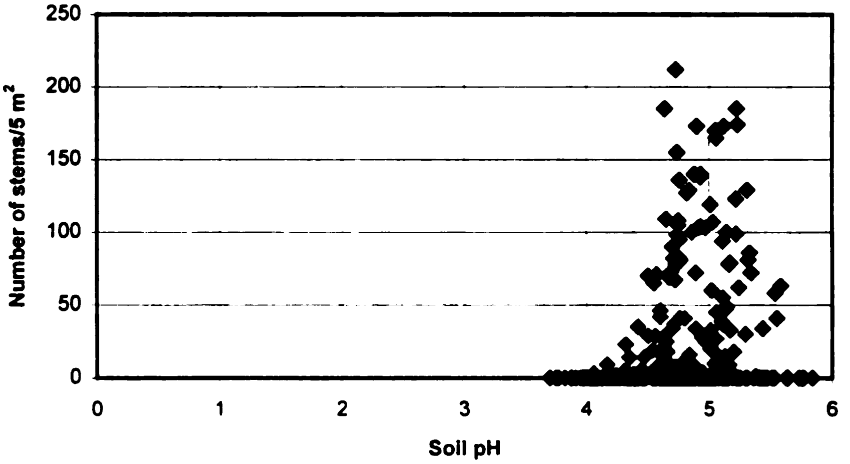


Figure 2. Scatterplot of lupine density on soil pH at Allegan State Game Area, MI, 1995.

---

[3] Plots that were within 1 meter of a road were excluded from this analysis due to the potential of confounding effects from material applied to and scattered from the road.

Regression of the PDL (the index of available light) on lupine density produced no statistically significant, simple linear relationship (adjusted r squared = 0.102) (Figure 3). This was also the case with flower[4] counts (adjusted r squared = 0.012). However, if the variables are truly unrelated, multiple regressions run on the resulting positive and negative residuals should also generate low adjusted r squared values (Thomson, *et al.*, 1996). Given the potentially large number of factors which may affect the suitability of a site for lupine, it would be unlikely to find a strong predictive relationship based on light alone. Factor-ceiling distributions partitioned regression was employed to identify the relationship between the upper limit of lupine density and light (Thomson, *et al.*, 1996). Using this iterative technique, density was repeatedly regressed on the positive residuals from the previous regression model (Table 2). The third and final[5] iteration produced a regression model which estimates the frontier line (upper boundary of the lupine density / PDL relationship) with an adjusted r squared of 0.739 (Figure 4).

---

[4] Because n was smaller for flowers than for stems and were highly correlated, stems were used for all further analysis.

[5] By this iteration, n equaled 20.

Table 2. Regression model statistics for each iteration of the factor-ceiling distributions partitioned regression for proportion of direct light vs. lupine stem density (number/5 m^2).

	n	Adjusted R^2	b	m	Actual F	Signif. F	p value for b	Accept/ Reject[1]
initial regression	443	0.102	5.4	50.1	51.281	3.370	0.096	reject
partition 1	110	0.238	43.7	96.2	34.989	3.953	0.000[2]	reject
partition 2	48	0.481	70.5	138.7	44.617	2.760	0.000[2]	reject
partition 3	20	0.739	96.5	160.9	54.873	7.200	0.000[2]	reject

[1] Accept/Reject null hypothesis H_0: y = b; where b= a constant. Reject because Actual F is greater than significant F.

[2] Significant at p=0.05

The Spearman's rho correlation coefficient, ($r_s = 0.572$; $p < 0.001$), between the PDL and the observed desiccation class was significant (Figure 5). Lupine plants remained greener for longer into the summer at lower PDL than at high proportion of direct light. This suggests that while a high PDL values may be associated with greater lupine stem densities, they also predict premature senescence during unusually dry years.

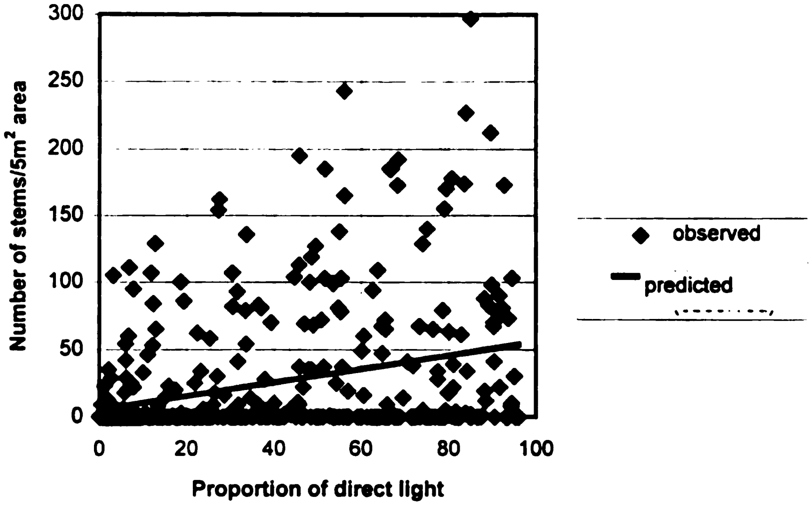


Figure 3. Scatterplot of stem density on proportion of direct light at Allegan State Game Area (ASGA), June-July 1995; "predicted" refers to the regression: stem density = 0.5007 (proportion of direct light) + 5.4351 (N = 443; adjusted r squared = 0.102).

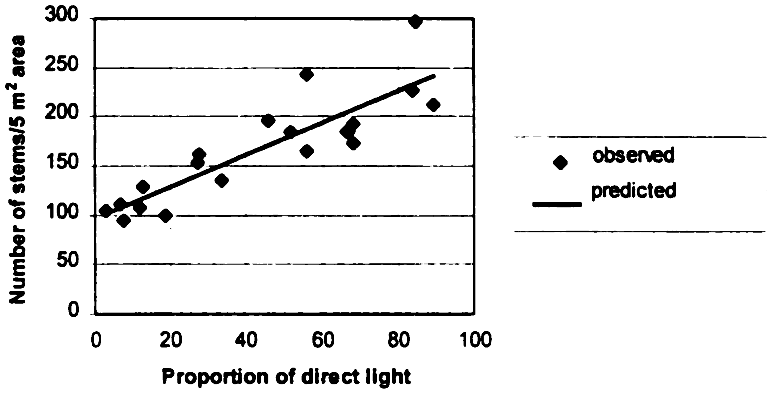


Figure 4. Scatterplot of stem density on proportion of direct light at Allegan State Game Area (ASGA), June-July 1995; "predicted" refers to the fitted frontier regression: stem density =1.6085 (proportion of direct light) + 96.538; (N = 20; adjusted r squared = 0.739).

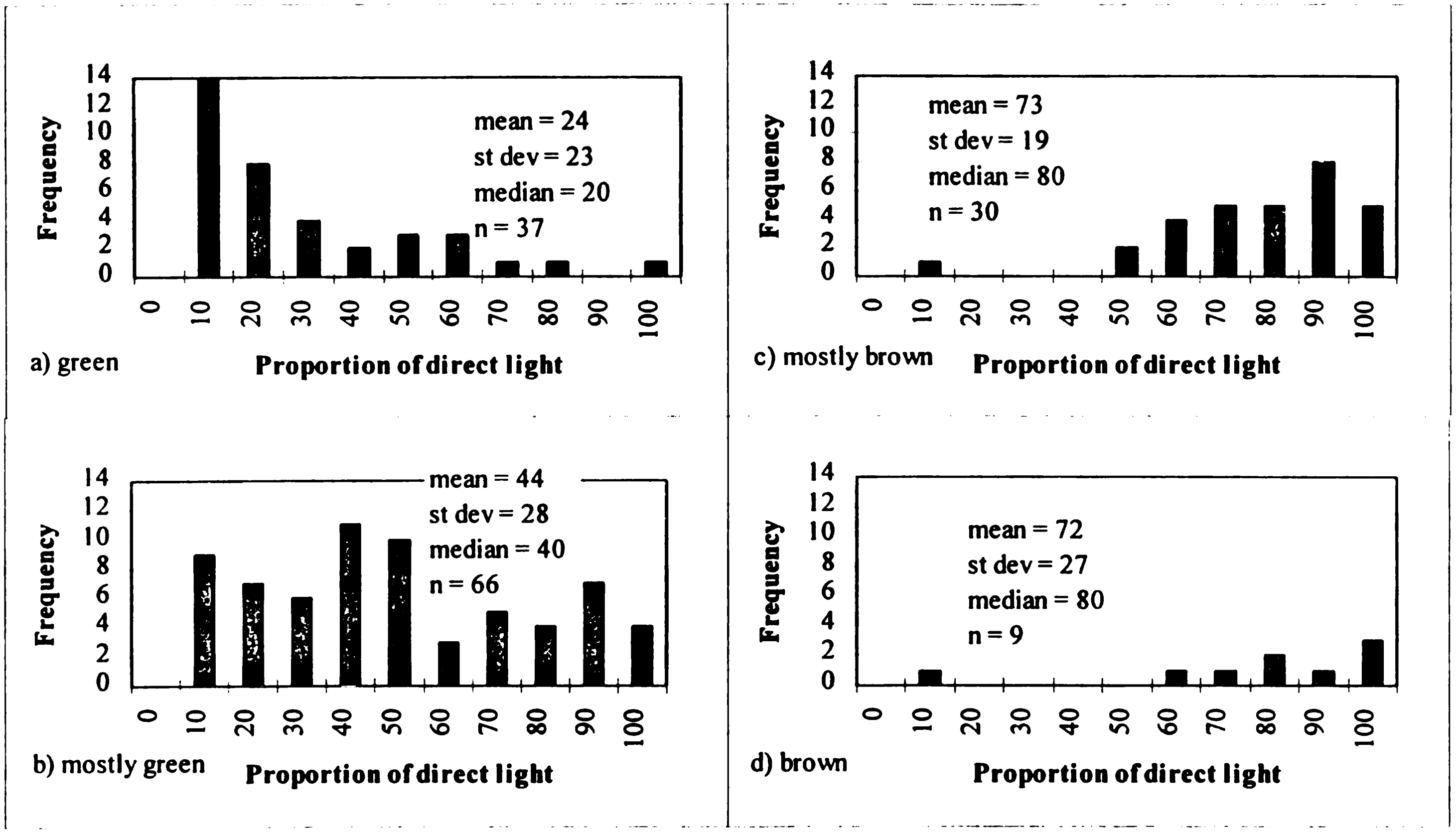


Figure 5. Histograms of the number of plots by proportion of direct light for four lupine foliar desiccation classes: a) green; b) mostly green; c) mostly brown; d) brown.

Greenhouse Study

Wet and dry leaf weight, dry root weight, and leaf area were measured because of their physiological significance for lupine and probable relationship to KBB. Dry leaf weight, dry root weight, root/shoot ratio (dry), and wet leaf/dry leaf mass ratio were significantly ($p < 0.01$) different among light treatments according to the Kruskal-Wallis test (Table 3).

The ratio of wet to dry leaf weight was greatest in 35% light (mean = 6.24), and smallest in 100% light (mean = 4.93). This implies that desiccation is more of a problem in areas with full sun exposure, and supports the results of the field study, indicating that shadier areas protect against desiccation. Additional supporting evidence is provided by the pattern of root to shoot ratio, which was greatest in 100% light (mean = 2.48), and smallest in 35% light (mean = 1.01). The fact that lupine plants growing in high light environments have relatively high root to shoot ratios suggests that they have adapted by proportionally reducing leaf surface area to decrease water loss, and increasing root surface area to increase water absorption.

However, plants were significantly ($p < .05$) larger under 100% light than in the shade treatments (Table 3). Leaf area follows a similar trend, but the relationship was not significant, probably due to variability among plants within treatments. This implies that the plants grow larger`11 under high light, potentially resulting in more food for the KBB, and possibly more competitive lupine plants. With larger roots, the plants would be better able to compete for nutrients and water. With larger leaves, they would have an advantage in competing for light and space.

Table 3. Effects of light on *Lupinus perennis* biomass when grown in a green house for 115 days; N = 41

	Mean Rank of Light Treatments			Means and Standard Deviations of Light Treatments			Statistics for All Treatments Combined				Kruskal Wallis Test Statistic[1]	
Variables (per/pot)	**35%**	**65%**	**100%**	**35%**	**65%**	**100%**	**Mean**	**Std. Dev.**	**Min**	**Max**	**Chi-square**	**Significance**
Dry leaf weight (g)	12.3	23.3	27.0	0.58 (± 0.33)	1.36 (± 0.82)	1.87 (± 1.27)	1.24	1.01	0.12	4.46	10.702	.005
Dry root weight (g)	7.8	23.7	31.1	0.51 (± 0.24)	1.96 (± 0.83)	3.37 (± 1.55)	1.94	1.52	0.12	5.23	25.839	.000
Leaf area(cm^2)	16.3	22.0	24.5	85.32 (± 63.98)	131.71 (± 82.44)	175.40 (± 136.38)	130.85	102.50	2.55	451.56	3.274	.195
Root/shoot (dry)	11.5	22.3	29.0	1.01 (± 0.42)	1.93 (± 1.38)	2.48 (± 1.29)	1.81	1.26	0.56	6.09	14.076	.001
Wet/dry (leaf)	29.3	18.5	15.5	6.24 (±1.11)	5.32 (± 0.86)	4.93 (± 0.87)	5.49	1.07	3.24	7.37	9.561	.008
Wet leaf weight (g)	14.1	23.0	25.6	3.89 (± 2.50)	7.33 (± 4.77)	9.74 (± 7.13)	7.00	5.54	0.42	23.89	6.690	.035

[1] degree of freedom = 2

Discussion

Managing vegetation (and indirectly managing available light) to provide habitat favorable to KBB appears to involve a balancing act. If KBB require some minimum amount of accessible lupine (yet to be identified), managers may strive to achieve a target lupine density to maximize KBB population size. If such a density target falls on the lupine density frontier, it is easy to identify a minimum level of light that would be required for lupine to have any chance of meeting this density criterion. However, it is also necessary to allow for a range of canopy densities and consequent light intensities in order to offer protection for the second generation larvae from complete lupine desiccation due to drought. In short, managers should provide habitat with a mix of optimal environmental conditions for lupine growth and conditions which provide protection for lupine (and thus, the butterflies) during years with "unusual" weather.

Because lupine are found exclusively on acidic soils at ASGA, it is not surprising that they are frequently found on soils enriched by the acidic litter of overstory canopies of oaks (and in other parts of KBB's range, pines). These tree species may serve to maintain low soil pH, particularly in areas with frequent fire. The fire regime likely to have been common in oak savannas in pre-settlement times would have tended to elevate soil pH (Tester, 1989). Judging by the narrow pH range within which lupine were found at ASGA, it appears that soil pH affects the distribution of lupine. Maintaining healthy lupine populations may require a combination of acidic conditions facilitated by overstory trees and periodic disturbance (primarily fire) that keeps competition levels low. There may also be a balance between lupine's light and soil pH requirements.

Individual trees often generate a pattern of soil pH in which values increase with distance from the base of individual trees, with the magnitude of this effect depending on tree species (Zinke, 1962). Given that preliminary investigations found lower soil pH under the forest canopy than in adjacent open areas (Mary Rabe, Michigan Department of Natural Resources, pers. Comm, 1996), one might assume that lupine would grow best near trees, unless limited by low light. The best sites for lupine appear to be sandy sites where both light and soil pH are favorable.

Another possibility is that the trees in oak savannas (and elsewhere in KBB's range, pine barrens) affect other environmental variables that in turn affect lupine growth and density. Because trees affect multiple environmental variables, (e.g., soil moisture, pH, nutrient levels and light) (Anderson, 1991; Crozier and Boerner, 1984) it is likely that the apparent correlation between light and lupine density may be the result of confounding factors.

Nutrient availability could be a significant issue in the relatively infertile savannas and barrens where lupine are found. Numerous studies have shown that soils under trees have significantly higher concentrations of organic matter, total and available N, Ca, K, P, Na, and S (Kellman, 1979; Belsky *et al.,* 1989; Young, 1989; Vetaas, 1992). Because lupine fix nitrogen from the atmosphere, they may not benefit from this elevated nutrient availability, and may in fact, be at a competitive disadvantage relative to non-nitrogen fixing vegetation.

As an early successional, nitrogen-fixing species, lupine may have developed an evolutionary strategy that is tailored to survival on depauperate, moisture-deprived, barren sites and improving such sites via nitrogen fixation. Lupine is probably at a competitive disadvantage on better sites. This nuance complicates interpretation of the positive association between lupine density and light. It could reflect a physiological light requirement, decreased competition from other plants in the nutrient or moisture-limited open areas, or a combination of these factors.

One artificial element of the greenhouse study design introduced some caveats that must be considered when interpreting results. All pots were watered when weighing indicated a soil moisture below 35%. Presumably due to greater evapotranspiration rates, plants in the 100% light treatment were watered more often than those in the 65% or 35% treatments. Under field conditions, lupine grow on sandy soil where available water may be limited, and the evapotranspirative stress characteristics of open areas (i.e. high light) would cause desiccation and perhaps premature senescence. Another complication introduced by the watering regime concerns nutrient availability. Because plants were watered with a fertilizer solution, plants which received more water also received more nutrients. If one or more nutrients were limiting, this would have unintended consequences by introducing an independent variable (nutrition) that was not part of the experimental design.

Conclusions

Light and soil pH appear to affect lupine growth and density. Results indicate that a pH range of 4.2 to 5.6 and the highest available light provide the best lupine habitat. However, because of the potential for weather extremes such as early summer drought and late spring frost, land managers protecting the KBB should aim to provide lupine habitat that covers a range of light levels. The easiest way to accomplish this goal is via management of stand density. The habitat diversity thus created is especially important for an endangered species. Managers need to be very cautious and not only provide the best habitat for lupine, but be certain to provide protection against unusual or extreme conditions.

Further research is needed to determine how much lupine is required to support KBB populations. This study provided information about two tree-dependent environmental variables and documented their relationship with lupine. Ultimately, this improved understanding of lupines requirements should lead to a more complete description of KBB's habitat requirements. Information on the effects of other environmental variables such as nutrient and water availability on lupine density would further improve a habitat model of lupine and the KBB.

BIBLIOGRAPHY

Andersson, T. 1991. Influence of stemflow and throughfall from common oak (Quercus robur) on soil chemistry and vegetation patterns. Canadian Journal of Forest Research 21:917-924.

Bess, J.A. 1989. Status of the Karner blue butterfly, Lycaeides melissa samuelis Nabokov, in the Manistee National Forest. Report to Michigan Natural Features Inventory, Lansing, Michigan 20 p. (unpublished).

Boyonoski, A.M. 1992. Factors affecting the establishment and maintenance of Lupinus perennis, (wild lupine). Unpublished M.S. Thesis, University of Guelph, Ontario.

Bray, J.R. 1955. The savanna vegetation of Wisconsin and an application of the concepts order and complexity to the field of ecology. Unpublished Ph.D. Dissertation. The University of Wisconsin, Madison. 251 p.

Chan, S.S., R.V. McCreight, J.D. Walstad, and T.A. Spies. 1986. Evaluating forest vegetative cover with computerized analysis of fisheye photographs. Forest Science 32:1085-1091.

Clark, J.S. 1991. Disturbance and population structure on the shifting mosaic landscape. Ecology 72:1119-1137.

Cowling, W.A., J.C. Clements. 1993. Association between collection site soil pH and chlorosis in Lupinus angustifolius induced by a fine-textured, alkaline soil. Australian Journal of Agricultural Research 44:1821-1836.

Crozier, Carl R., and E. J. Boerner. 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. Oecologia 62:337-343.

Cryan, J.F., and R. Dirig. 1978. A report on the status of the Karner blue butterfly (Lycaeides melissa samuelis Nabokov) in New York State. Report for the New York State Department of Environmental Conservation. August 29, 1978. 18 p.

Curtis, B. 1959. The vegetation of Wisconsin. The university of Wisconsin press. Madison, Wisconsin. 657 p.

Dirig, Robert. 1973. The endangered Karner blue. The Conservationist 28:6,47.

Dirig, Robert. 1988. Nabokov's blue snowflakes. Natural History 97:68-69.

Haack, R.A. 1993. The endangered Karner blue butterfly (Lepidoptera: Lycaenidae): Biology, management considerations, and data gaps. Proceedings of the 9th

Central Hardwood Forest Conference. U.S.D.A.-Forest Service, North Central Forest Experiment Station. St. Paul, Minnesota. p. 83-100.

Herms, Catherine P. 1996. The endangered Karner blue butterfly (Lepidoptera: Lycaenidae) in Michigan: Habitat suitability, potential impacts of gypsy moth (Lepidoptera: Lymantriidae) suppression and laboratory rearing. Unpublished Masters Thesis, Department of Entomology, Michigan State University.

Holland, V.L. 1973. A study of soil and vegetation under Quercus douglasii compared to open grassland. Unpublished PhD. Dissertation, Department of Botany, University of California, Berkeley. 359 p.

Hultman, G. 1978. Trees, Shrubs, and Flowers of the Midwest. Great Lakes Living Press, Chicago. 77 p.

Loehle, Craig, and G. Wein. 1994. Landscape habitat diversity: A multiscale information theory approach. Ecological Modeling 73:311-329.

Maxwell, J., and T. Givnish. 1993. Research on the Karner blue butterfly at Fort McCoy, Wisconsin: Progress report for the 1993 field station. Report submitted to the US Fish and Wildlife Service, and the Department of the Army. 22 p.

Parker, V.T., and C.H. Muller. 1982. Vegetation and environmental changes beneath isolated live oak trees (Quercus agrifolia) in a California Annual Grassland. American Midland Naturalist 107:69-81.

Pickering M.G., and S.B. Gebauer. 1993. Status report: Assessment of associations between lupine population characteristics and vegetation and soil characteristics - 1991-92. Eastern New York Chapter of the Nature Conservancy. (unpublished)

Rabe, M. 1995. Personal communication.

Rich, P.M. 1989. A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory. Los Alamos, New Mexico. 80 p.

Shuey, J.A., J.V. Calhoun, and D.C. Iftner. 1987. Butterflies that are endangered, threatened, and of special concern in Ohio. Ohio Journal of Science 87:98-106.

Smallidge, P.J., and D.J. Leopold. 1992. Environmental factors and critical habitat for Lycaeides melissa samuelis along transmission line rights-of-way in east-central New York, USA.(Draft).

Spies, T.A., W.S. Ripple, and G.A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555-568.

Stewart, M.M., and C. Ricci. 1988. Dearth of the blues. Journal of Natural History 92: 64-70.

Tang, Caixian, J. Kuo, N.E. Longnecker, C.J. Thompson, and A.D. Robson. 1992. High pH causes disintegration of the root surface in Lupinus angustifolius L. Annals of Botany 71:201-207.

Tang, Caixian, and A.D. Robson. 1993. pH above 6.0 reduces nodulation in Lupinus species. Plant and Soil 152:269-276.

Thomson, James, D.G. Weiblen, B.A. Thomas, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. Ecology 77:1698-1715.

Welch, Robert J. 1993. Dispersal and colonization behavior in the Karner blue butterfly (Lycaeides melissa samuelis) in central Wisconsin. Final Report to U.S. Fish and Wildlife Service. Green Bay, Wisconsin. 50 p.

Wisconsin Department of Natural Resources Karner Blue Technical Team. 1993. 3rd draft: Wildlife Management Guidelines for Karner blue. (unpublished).

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.

Chapter 3

The Effect of Landscape Level Spatial Parameters and Forest structure on the distribution of *Lupinus Perennis* and *Lycaeides melissa samuelis* Nabokov.

Abstract

The Karner blue butterfly (KBB), *Lycaeides melissa samuelis* Nabokov, (Lepidoptera: Lycaenidae) was added to the federal endangered species list in December 1992 following a period of extensive habitat decline. To restore remnant populations of Karner blue butterflies to sustainable levels, land managers need to consider the impacts of their actions on lupine, the Karner blue's sole larval food plant. Because KBB fits in a metapopulation model, I expected that the spatial parameters of the KBB's habitat would affect its prospects for survival. In forested landscapes, spatial metrics (e.g., amount of edge, connectedness of habitat patches, distance between habitat areas, patch shape and patch size) have been directly linked to flora and fauna species composition. In this study, exploratory analysis of stand data and lupine and KBB distribution was conducted to determine (1) if the landscape properties required by KBB could be identified and (2) if characteristics of forest stands could be linked to KBB habitat requirements. To do this, stand (e.g., species, age, and size class) and landscape (e.g. patch size, density, and shape, and nearest neighbor) characteristics were contrasted for two comparisons: (1) for stands where lupine was absent (LA) and stands where lupine was present (LP), and (2) for stands where lupine was present and KBB was absent (LPKA) and stands where lupine and KBB were present (LPKP). Overall, LPKP patches tended to be closer to one another, more complex, and larger than LPKA. Stands of medium density contained more LPKP sites than LPKA sites. LP areas were more likely to be in the low stand density class and much less likely to be in the high stand density class than LA.

Introduction

The Karner blue butterfly (*Lycaedies melissa samulis*) (KBB) was added to the federal endangered species list in December 1992 following a period of extensive habitat decline (Haack, 1993; Dirig, 1988). Scientists have long known that habitat preservation is the key to species preservation (e.g., Loehle and Wein, 1994). This is particularly evident in the case of the Karner blue butterfly, one of the most habitat dependent species in the northeastern US (Dirig, 1988). Recently, scientists have been working on a habitat description for the Karner blue. In Michigan, the habitat has been described as oak savanna with an understory of lupine and other nectaring plants (Pickering and Gebauer, 1993; Shuey, *et al.*, 1987; Welch, 1993). Because this description does not address such specifics as the amount of lupine required, the size, shape, and distribution of suitable areas, or the ecological requirements of lupine, managers lack a critical tool for restoring KBB populations. The first goal of this research is a more precise description of the spatial component of Karner blue's habitat requirements.

The savanna type has been described as a structurally simple, seasonally water-stressed community with a sparse overstory of trees and shrubs that forms structural discontinuities above the grassland (Belsky and Canham, 1994). Trees invade savannas via seeds dispersed by wind and animals and by clonal spread from adjacent woodlots. In pre-settlement times, the size and age structure, species diversity, and dynamics of savanna vegetation were controlled by local and regional scale disturbances such as fire (low intensity surface, as well as "stand-replacing" fire), weather (e.g., wind-throw, tornado), and herbivory. Savannas can only be maintained by a relatively high frequency of these succession-interrupting disturbances (Tester, 1989). The oak savanna forest type favored by the Karner blue has become increasingly rare due to fire exclusion (Welch, 1993; Shuey, *et. al.*, 1987) and increasing urbanization (Givnish, *et al.*, 1988; Smallidge and Leopold 1992; Cryan and Dirig 1978). The Karner blue is now commonly found within small patches of *L. perennis* resulting from human disturbance such as along gas pipeline rights-of-way, trails, roads, and abandoned farm fields (Haack, 1993).

To restore remnant populations of Karner blue butterflies to sustainable levels, land managers need to consider the impacts of their actions on lupine, the Karner blue's sole larval food plant (Haack, 1993; Smallidge and Leopold, 1992; Stuart and Ricci, 1988; WI DNR, 1993). *Lupinus perennis* is a member of the pea family and is the only lupine native to the eastern US (Hultman, 1978). A better understanding of lupine's ecological requirements is a critical first step towards managing the recovery of the Karner blue. Lupine habitat is likely affected by trees (e.g., light, soil moisture, soil chemistry). It is therefore possible that lupine habitat can be described at a landscape level as relationships among forest variables such as size class and age class. Another goal of this research is to see whether these relationships exist.

Structure and connectivity are two classes of landscape properties which control the distribution of species over the landscape (Forman and Godron, 1986; LaGro, 1991). Structural properties include the shape, size, and juxtaposition of habitat patches (Burgess and Sharpe, 1981; Forman and Godron, 1986). Connectivity properties affect the potential for movement of organisms within a landscape (Baudry and Merriam, 1988; Janssens and Gulinck, 1988).

Landscape connectivity can be influenced by the proportion of the landscape in so-called "edge" communities which differ from those found in "pure" cover types (Malcolm, 1994). The proportion of a patch characterized as edge varies with patch structure (e.g., shape and size of the patch) (LaGro, 1991). Small patches may consist entirely of edge-modified habitat (Kapos, 1989). The effects of edge may extend far into convoluted patches, ultimately changing landscape connectivity (Alverson, et al., 1988; Janzen, 1983; Johnson, et al., 1981; Kapos, 1989; Noss, 1983; Ramney, et al., 1981; Temple and Cary, 1988). Edge may play an important role for KBB management by providing effective connectivity between habitat patches not previously recognized by scientists and land managers as connected or connectable.

In forested landscapes, amount of edge, connectedness of habitat patches, distance between habitat areas, patch shape and patch size have been directly linked to flora and fauna species composition (Franklin and Forman, 1987; Harris, 1984; Thomas, 1979). For many species, the spatial extent of landscape properties that affect habitat quality may be many times greater than the aggregate of the home ranges of the individuals within a population (Gustafson, *et al.,* 1994). Landscape properties can also influence the suitability of individual patches (Bach, 1988). For example, diversity of wintering bird populations found within individual patches was found to be a landscape level function determined by distribution of habitat within the forest matrix (Pearson, 1993).

Habitat fragmentation produces isolated patches, with an increased likelihood of deme extinction due to a lack of immigration possibilities, particularly for smaller patches with low carrying capacities (Harrison, 1991; Miles, 1994). Agriculture, urbanization, and forestry practices have substantially altered the pre-settlement land cover patterns over the past century, resulting in a landscape consisting of a mixture of patches generated by natural processes and human activities (Krummel et al., 1987). A better understanding of how this mixture of patches affects species composition at the landscape level is critical if preservation efforts are to be successful (Loehle and Wein, 1994). The effect of landscape properties on metapopulation dynamics appears likely to be important in the case of the Karner blue,

A metapopulation is a set of populations persisting over space and time via waxing and waning, extinction and recolonization (Harrison, 1991). Four broad types of metapopulations have been theorized: source-sink, patchy, non-equilibrium, and classical. In the source-sink model, source demes are considered critical to metapopulation maintenance, while sink demes are inconsequential or a hindrance in terms of survival. In patchy metapopulations, high rates of dispersal tend to demographically unite highly fragmented landscapes. Non-equilibrium metapopulations tend to decline due to low recolonization relative to extinction. Classical metapopulations are those where a dynamic balance between colonization and extinction is maintained (Harrison, 1991).

Harrison (1991) suggests the non-equilibrium model as the best fit for the Karner blue on the grounds that the ongoing reduction of their habitat can only lead to extinction. Others have suggested that small, isolated populations of Karner blue are often at risk of local extinction from random demographic events when there is no replenishing effect due to immigration from nearby populations (e.g. Givnish *et al.*, 1988). However, these dynamics may be relatively recent. Though the Karner blue has low motility (less than 1.5 km) (Haack, 1993), the species has long thrived on lupine patches that were constantly shifting in both time and space due to fire, herbivory, and succession (Haack, 1993; Smallidge and Leopold, 1992). A continuous series of local extinctions from and recolonizations of these shifting patches of habitat probably accounts for the ongoing stability of Karner blue metapopulations in such dynamic environments. These dynamics would only have been possible with a high degree of patch connectivity (Harrison, 1991). This implies that Karner blue metapopulations may be better fit by the patchy model. ✓

Local population (also known as deme) extinction and habitat patch recolonization are central to metapopulation models (Harrison, 1991). Because both processes depend on the spatial distribution of demes within a metapopulation, landscape structure and connectivity are critical variables. For example, larger islands produce more migrants, the probability of immigration decreases exponentially with distance, and the probability of extinction is inversely related to the carrying capacity of the patch (Gilpin, 1987). Thus an understanding of the spatial parameters of KBB habitat is critical for managing and sustaining KBB metapopulations.

Deme extinction depends on genetic, demographic, and environmental forces acting within the patches (Gilpin, 1987). For example, genetic stochasticity (the loss of heterozygosity through drift and inbreeding), a frequent result of patch isolation, increases the risk of deme extinction (Harrison, 1991).

Movement of individuals among patches is critical for maintaining stable populations via recolonization (Backs and Eisfelder, 1990; Ellis and Lewis, 1967) and is dependent on landscape connectivity (Baudry and Merriam, 1988; Gilpin, 1987; Janssens and Gulinck, 1988). By itself, this would imply that managers should strive for connectivity. But, environmental stochasticity may have a greater influence on metapopulations than genetic stochasticity because it can affect and synchronize many demes simultaneously across the landscape (Comins and Noble, 1985; Harrison, 1991; Hastings and Wolin, 1989; Pacala, 1989; Shugart, 1984; Turner et al., 1989; Warner and Chesson, 1985). Therefore, it may also be very important to maintain unconnected refuges which can act as population sources following metapopulation extinction brought on by localized catastrophic events (Harrison, 1991).

The Karner blue exemplifies species requiring such a balancing act. Although Karner blue demes are spatially distinct, exchange of genetic material is believed to occur among them as a result of dispersal (Givnish, *et al.*, 1988; Maxwell and Givnish, 1993). Because Karner blue habitat can only be maintained through disturbance (e.g., fire, which is lethal to Karner blue individuals at all stages in their life cycle), a Karner blue metapopulation's risk of total extinction may be reduced by a horizontally complex distribution of habitat across the landscape (Maxwell and Givnish, 1993). Thus the best landscape structure may require a balance between connectivity and patch isolation.

Assuming that KBB is well represented by a metapopulation model, the survival of this species is likely to be affected by landscape properties such as structure and connectivity. Land managers have lacked information about the linkage between KBB metapopulation structure and the effect of their management on landscape properties. It is particularly important to understand the relationship between landscape structure/connectivity and metapopulations because the ultimate conservation goal for this species is a shift from the non-equilibrium to the patch metapopulation model via management of landscape structure and habitat quality. Exploratory analysis of stand data and lupine and KBB distribution was conducted to determine (1) if landscape properties required by KBB could be identified and (2) if characteristics of forest stands could be linked to KBB habitat requirements.

Methods

Data processing and analysis

Allegan State Game Area (ASGA) in southwest Michigan's Allegan County was selected as the location for this study because it is one of the two major areas in Michigan where Karner blue are found today, and is the only Michigan area for which spatially referenced information was available at the initiation of this study. Stand boundary and attribute data were provided by game area managers. Locations at which lupine were observed in 1995 and locations where KBB were observed over the past decade were digitized. While lupine has been observed throughout ASGA, KBB sightings have been confined to lupine patches south of the Kalamazoo River (Figure 7), possibly due to the river forming a recently insurmountable barrier to movement of KBB. For this analysis, I considered (1) lupine patches south of the Kalamazoo river habitat as one metapopulation of KBB and (2) lupine patches north of the river as unutilized potential habitat for a second KBB metapopulation. A key question was whether or not there are landscape properties associated with lupine patches north of the river which preclude utilization by the KBB.

The ASGA stand coverage was provided in a proprietary GIS format (C-map). This data was converted to an Arc/Info vector coverage. Because the stand information provided in this coverage (e.g. size and age class, and predominant overstory species) was lumped into one attribute, reclassification was required to generate stand attributes (Table

4) suitable for use as query criteria and subtotal categories. The approximate geographic locations of KBB sightings from this decade and 1995 lupine observations were recorded on and provided as a paper map[6]. Approximate on-screen digitizing[7] was employed because the paper map was of "field quality" and subject to distortions which would have severely limited the accuracy of coverages generated by tablet digitizing or scanning methods. Once completed, these vector coverages (Table 4) were converted to a raster format with a 15.23 m cell size (deemed adequate given the limited accuracy of the source coverages). I analyzed the lupine and KBB data at the stand level (e.g., if any portion of a lupine stand was coded as having lupine present, it was coded as lupine present (LP)) for two reasons : (1) more confidence in accuracy of stand boundaries than patch boundaries for lupine or KBB; (2) stands are the level of resolution at which forest vegetation is managed.

---

[6] Provided by Mary Rabe at The Michigan Natural Features Inventory

[7] Using the ASGA coverage as a backdrop, lupine and KBB patches were sketched on screen with a mouse. These resulting polygons were attributed and built into vector coverages.

Table 4. Geographic information system (GIS) coverages and associated attributes used to analyze landscape properties and their relationship to KBB and lupine habitat at Allegan State Game Area, Allegan Michigan, 1995.

Variable	Variable Type	Data Type	Classification Codes	Source
Tree density	independent	ordinal	0-non forest 1-low 2-medium 3-high	ASGA[1] stand map
Tree size	independent	ordinal	0-non-forest 1-sapling 2-pole timber 3-saw timber	ASGA stand map
Lupine	dependent/ independent	nominal	0-lupine absent 1-lupine present	on-screen digitizing of MINFI[2] paper map overlay on ASGA stand boundaries and reclass of ASGA stands
Karner blue butterfly	dependent	nominal	1-lupine present, KBB absent 2- lupine present, KBB present	on-screen digitizing of MINFI paper map overlay on ASGA stand boundaries and reclass of ASGA stands

[1] ASGA - Allegan State Game Area

[2] MINFI - Michigan Natural Features Inventory

Stand (e.g., species, age, and size class) and landscape (e.g., patch size, density, and shape; and nearest neighbor) characteristics were contrasted for two comparisons: (1) for stands where lupine was absent (LA) and stands where lupine was present (LP), and (2) for stands where lupine was present and KBB was absent (LPKA) and stands where lupine and KBB were present (LPKP) (Figure 7). Stand characteristics were also summarized for all stands (AS) to provide a baseline for comparison. The landscape characteristics were generated by processing GIS coverages with FRAGSTATS software[8]. Two new coverages were generated by reclassifying the stands coverage according to the values of the lupine and KBB attributes (Table 4, Figure 6). Two types of spatial metrics were used: those calculated at the level of the individual patch (e.g., area, patch density, size and shape, and edge metrics) and those which quantify spatial relationships among patches and the surrounding matrix (e.g., nearest neighbor metrics) and are calculated at the landscape level (McGarigal and Marks, 1993).

---

[8] FRAGSTATS version 2, Unix raster version by Kevin McGarigal and Barbara J. Marks. 1995

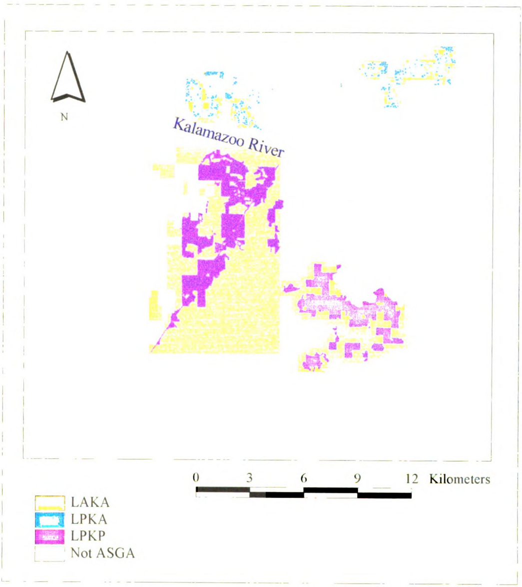


Figure 6. Map of areas with lupine present, KBB present (LPKP); areas with lupine present, KBB absent (LPKA), and areas with lupine absent, KBB absent (LAKA) at Allegan State Game Area (ASGA), Allegan, MI 1995.

The patch indices were grouped by class (e.g., AS, LA, LP, LPKA, LPKP). Class area (CA)[9] (in ha) and percent of total landscape area (PCTLAND)[10] were used to describe the area of each class. Although area metrics do not quantify landscape pattern, they do quantify landscape composition (McGarigal and Marks, 1993) which may prove important to KBB. Patch density, size, and variability metrics include number of patches (NP)[11], patch density (PD)[12] (#/100 ha) and mean patch size (MPS)[13] (ha). Edge is another metric quantified at the patch level. Edge density (ED)[14] has the advantage of removing the issue of differences in class area. Because shape is difficult to quantify, I focused on two indices which characterize shape-related properties. The first, edge to area ratio, captures complexity but not morphology. The area weighted mean shape index (AWMSI)[15] statistic calculated in FRAGSTATS was appropriate for this study

---

[9] $\mathrm{CA} = \sum_{j=1}^{n} a_{ij}\left(\frac{1}{10{,}000}\right)$ where a_{ij} = area (m^2) of patch j in class i; n = number of patches in the landscape

[10] $\mathrm{PCTLAND} = \frac{\sum_{j=1}^{n} a_{ij}}{A}$ where A = total landscape area (m^2)

[11] $\mathrm{NP}_i = n_i$ where n_i = number of patches in the landscape of patch type (class) i..

[12] $\mathrm{PD}_i = \frac{n_i}{A}(10{,}000)(100)$

[13] $\mathrm{MPS}_i = \frac{\sum_{j=1}^{n} a_{ij}}{n_i}\left(\frac{1}{10{,}000}\right)$

[14] $\mathrm{ED} = \frac{\sum_{k=1}^{m'} e_{ik}}{A}(10{,}000)$ where m' = number of patch types (classes) present in the landscape; e_{ik} = total length (m) of edge in landscape between patch types (classes) i and k.

[15] $\mathrm{AWMSI} = \sum_{j=1}^{n}\left[\left(\frac{.25p_{ij}}{\sqrt{a_{ij}}}\right)\left(\frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}}\right)\right]$ where p_{ij} = perimeter (m) of patch j of class i.

because the areas of stands with LA, LP, LPKP, and LPKA are not equal. The other shape metric used was fractal dimension. This involves the relationship $A = kP^{\frac{2}{D}}$, where P = perimeter; D = the fractal dimension; k = a constant; A = area. As shapes become more complex, D approaches 2 (Burrough, 1986; McGarigal and Marks, 1993). The area weighted statistic (area weighted mean patch fractal dimension, AWMPFD)[16] is the recommended technique for use with small sample sizes, (in our case n < 20).

At the landscape level, two nearest neighbor statistics were calculated to test for an effect from being near another like patch (e.g., does it matter to KBB if patches of suitable habitat are near each other or not?). Mean nearest neighbor (MNN)[17] was used to determine concentration levels of patch types and nearest neighbor standard deviation (NNSD)[18] was used to describe the regularity of patch distribution within classes, that have nearest neighbors.

---

[16] $\text{AWMPFD} = \sum_{j=1}^{n} \left[\left(\frac{2 \ln(.25 p_{ij})}{\ln a_{ij}} \right) \left(\frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}} \right) \right]$

[17] $\text{MNN} = \frac{\sum_{j=1}^{n'} h_{ij}}{n'_i}$ where h_{ij} = distance (in meters) from patch j in class i to the nearest neighboring patch of class i, based on edge-to-edge distance; n'_i = number of patches in the landscape of patch type (class) i

[18] $\text{NNSD} = \sqrt{\frac{\sum_{j=1}^{n'} \left[\left(h_{ij}\right) - \left(\frac{\sum_{j=1}^{n'} h_{ij}}{n'_i} \right) \right]^2}{n'_i}}$

The raster coverages for lupine and KBB presence generated in Arc/Info were converted to ERDAS image file format and processed by FRAGSTATS. Global parameters used in FRAGSTATS included core area = 10 m, travel distance = 1 km, and diagonal travel allowed. FRAGSTATS output was imported to a spreadsheet[19] format for additional analysis and summarization of results. Two sample t-tests were used to statistically compare the output of the FRAGSTATS analysis for the patch level statistics.

To determine if a relationship existed between forest properties and KBB and lupine distribution, I plotted histograms in Arc View for each pair of comparisons. The amount of area corresponding to each category (e.g., LA, LP, LAKA, and LAKP) in each class of each forest variable (e.g., size class, species, density class) was transformed to a percentage of total area for plotting in bar charts.

---

[19] Microsoft Excel version 7

Results

Stands where lupine and KBB are both present comprise a larger area (2274 ha) than stands where lupine are present and KBB are absent (729 ha) (Table 5). It is possible that the aggregate size of lupine patches north of the Kalamazoo river may be too small to support a metapopulation. The mean patch size (MPS) for all continuous lupine patches (across stand boundaries) (53.6 ha) is less than that for lupine patches with KBB (88.3) but the difference is not statistically significant ($p = 0.05$).

Table 5. Class level pairwise comparisons[1] of spatial statistical output from FRAGSTATS for areas with lupine absent (LA), lupine present (LP), lupine present and KBB absent (LPKA), and lupine and KBB both present (LPKP).

	Area metrics		**patch density, patch size, and variability metrics**			**Edge metric**	**Shape metric**		**Nearest neighbor metrics**	
TYPE	Class area (ha)	Percent land (%)	Number of patches (#)	Patch density (#/100 ha)	Mean patch size (ha)	Edge density (m/ha)	Area weighted mean shape index	Area weighted mean patch fractal dimension	Mean nearest neighbor (m)	Nearest neighbor standard deviation (m)
LA	17761	85.48	53	0.07	335.1	5.83	4.60	1.16	125.4	123.7
LP	3017	14.52	40	0.05	75.4	3.44	4.46	1.18	139.2	199.3
LPKA	729	3.51	20	0.03	36.4	1.08	2.98	1.15	208.5 [2]	259.2
LPKP	2288	11.01	20	0.03	114.4	2.36	4.93	1.19	69.9	51.8

[1] comparisons made between LA and LP, and between LPKA and LPKP.

[2] Means of LA and LP are significantly different ($p < 0.05$) for the two tailed two sample students-t test.

Patches where lupine and KBB are present have an edge density which is more than two times as large as lupine patches with no KBB (2.4 m/ha vs.1.1 m/ha), implying that KBB may slightly favor a preponderance of edge. AWMSI for LPKP patches (4.95) was not significantly different than for LPKP patches (2.99). Stands with LPKP were more concentrated ($p < 0.05$) (mean nearest neighbor (MNN) = 69.9 m) and more regular (nearest neighbor standard deviation (NNSD) = 57.8 m) than LPKA (MNN = 208.1 and NNSD = 259.2).

I considered the frequency of stands by overstory density class for the qualifications: 1) all stands, 2) lupine absent, 3) lupine present, 4) lupine present, KBB absent, 5) lupine and KBB present (Figure 7). Although both lupine and KBB can be found in every overstory density class, there appears to be a negative relationship between overstory density and the likelihood that a stand will contain lupine and KBB (Figure 7). However, both lupine and KBB are more likely to be present in low density forest than in open grassland, implying that optimal conditions do not include light levels associated with 100% sky. I also compared the frequency of stands by overstory size class for the qualifications: 1) all stands, 2) lupine absent, 3) lupine present, 4) lupine present, KBB absent, 5) lupine and KBB present. The relationships did not appear as clear as they did with the density classes (Figure 8). It appears that LPKP areas are relatively more prevalent under grass and sapling size classes than LPKA, while LPKA have more area in the larger size classes than LPKP areas.

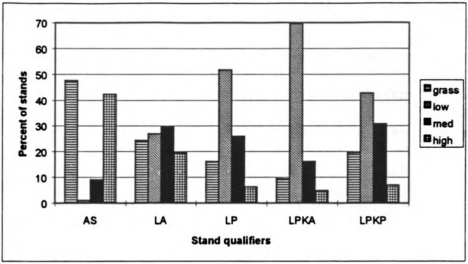


Figure 7. Frequency of stands by density class for the qualifiers: all stands (AS), lupine absent (LA), lupine present (LP), lupine present, KBB absent (LPKA), and lupine present, KBB present (LPKP) at Allegan State Game Area, Allegan, MI, 1995.

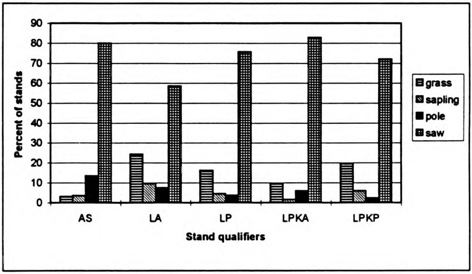


Figure 9. Frequency of stands by size class for the qualifiers all stands (AS), lupine absent (LA), lupine present (LP), lupine present, KBB absent (LPKA), and lupine present, KBB present (LPKP) at Allegan State Game Area, Allegan, MI, 1995.

Discussion

There appears to be a negative relationship between tree density and both lupine and KBB, yet both are able to survive amongst large trees. I think the density relationship is indicative of a positive correlation with light. However, both lupine and KBB appear to prefer low density forest to open grassland, implying that the optimal light threshold is less than 100 percent. I also think this is good news for forest managers with KBB on their land. Through careful thinning, they can provide for the butterflies' needs (lupine) as well as continue producing timber. In fact, I think that although lupine and KBB appear to be more common in low density stands than grassland and higher density forest stands, it may be wise to manage for a mosaic of stands with differing densities. This will provide ample habitat with high light levels and protected areas to serve as lupine refugia during years with early summer drought or late spring frosts.

I think my results demonstrate that the spatial arrangement of these lupine patches is important based on the nearest neighbor results which showed the area which sustains a KBB metapopulation has patches that are statistically closer to one another. This means that managers attempting to perpetuate a metapopulation of KBB will need to manage the forest from the landscape level. This entails coordinating preservation efforts with regards to size, edge, and connectivity.

Based on the two potential metapopulations studied, it appears that over 2000 ha of habitat with a large proportion of edge is necessary. Connectivity also seems to be important. It appears that individual patches of habitat which are intended to be an active part of the metapopulation should be approximately 100 m apart from one another or closer. However, in keeping with metapopulation theory and concerns about extinction, some patches of KBB should be maintained at a distance greater than 70 m from the rest of the metapopulation to provide some protection against localized catastrophic events.

This study only included two distinct areas for analysis. Many of the comparison were not statistically significant ($p > 0.1$), however metapopulations of KBB are quite rare so the opportunities to conduct replicated experiments are limited. This research represents a starting point towards building a knowledge base about these ecological relationships. To develop a metapopulation model, further research is suggested in the following areas. First, KBB demographic information must be collected. Second, in this study, I defined KBB habitat solely by the presence or absence of lupine, however, KBB is known to have other requirements including ants and nectar sources (Haack, 1993). These must be mapped and included in habitat model-building. Third, information about KBB flight potential through different forest types is needed. For example, can KBB travel as far in high density forests as in low density forests, how far can they travel without relying on nectar sources? In the interim, studies similar to the one presented here should be carried out for other KBB metapopulations to further test the hypotheses advanced here.

Conclusions

I achieved my goals of developing a more precise description of the spatial component of KBB habitat and exploring the relationships between lupine and forest stand characteristics. Much work remains, but this study constitutes a good beginning because it provides information about spatial parameters likely to affect metapopulation dynamics, and forest attributes that affect KBB habitat quality. LPKP patches tend to be closer to one another than LPKA patches. LPKP patches are more common in medium density stands than are LPKA patches and LP patches were more likely to be in the low forest density class and much less likely to be in the high density class than were LA patches.

Although managing a forest for multiple use and for KBB protection may appear challenging, a GIS containing vegetation attributes can facilitate this process. I do not suggest that managers should attempt to achieve an exact match to the landscape parameters for the KBB metapopulation described in this paper; however, they may be a good first approximation. I think the relationship among trees, lupine and KBB distribution should be investigated further and that the spatial parameters should be tested for other KBB metapopulations.

BIBLIOGRAPHY

Alverson, W.S., Waller, D.M., and Solheim S.S., 1988. Forest too deer: Edge effects in northern Wisconsin. Conservation Biology 2:348-358.

Bach, C.E., 1988. Effects of host plant patch size on herbivore density: Underlying mechanisms. Ecology 69:1103-1117.

Backs, S.E., and Eisfelder, C.H., 1990. Criteria and guidelines for wild turkey release priorities in Indiana. Proceedings of the National Wild Turkey Symposium 6:134-143.

Baudry, J., Merriam, H.G., 1988. Connectivity and connectedness: Functional versus structural patterns in landscapes. Connectivity in Landscape Ecology. Proceedings of the 2nd International Seminar of the International Association of Landscape Ecology p. 3-28.

Belsky, A.J., Amundson, R.G., Duxbury, J. M., Riha, S.J., Ali, A.R., and Mwonga, S.M., 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26:1005-1021.

Belsky, A.J., and Canham, C.D., 1994. Forest gaps and isolated savanna trees: An application of patch dynamics in two ecosystems. BioScience 44:77-84.

Burgess, Robert L., Sharpe, D. M., and Bruner, M.C., 1981. Forest island dynamics in man-dominated landscapes. Eds. Burgess, R. L. and Sharpe, D. M. New York, Springer-Verlag. 310 p.

Comins, H.N., and Noble, I.R., 1985. Dispersal, variability, and transient niches: Species coexistence in a uniformly variable environment. American Naturalist 126:706-723.

Crozier, Carl R., and Boerner, E.J., 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. Oecologia 62:337-343.

Cryan, J.F., and Dirig, R., 1978. A report on the status of the Karner blue butterfly (Lyceides melissa samuelis Nabokov) in New York State. Report to the U.S. Fish and Wildlife Service.

Dirig, Robert., 1988. Nabokov's blue snowflakes. Natural History 97:68-69.

Ellis, J.E., Lewis, J.G., 1967. Mobility and annual range of wild turkeys in Missouri. Journal of Wildlife Management 31:568-581.

Forman, R.T.T., and Godron, M., 1986. Landscape Ecology John Wiley and Sons. New York, New York. 619 p.

Franklin, J.F., and Forman, R.T.T., 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecology 1:5-18

Gilpin, Michael E., 1987. Metapopulation structure and population vulnerability. In: Viable populations for conservation. Cambridge University Press. New York, New York. p 125-139.

Givnish, T.J., Mengis, E.S., and Schweitzer, D.F., 1988. Minimum area requirements for long-term conservation of the Albany Pine Bush and Karner blue butterfly: An assessment. (unpublished).

Gustafson, Eric J., Parker, G.R., and Backs, S.E., 1994. Evaluating spatial pattern of wildlife habitat: A case study of the wild turkey (Meleagris gallopavo). Midland Naturalist 131:24-33.

Haack, R.A., 1993. The endangered Karner blue butterfly (Lepidoptera: Lycaenidae): Biology, management considerations, and data gaps. Proceedings of the 9th Central Hardwood Forest Conference. U.S.D.A. -Forest Service, North Central Forest Experiment Station. St. Paul, Minnesota. p. 83-100.

Harris, L.D., 1984. The Fragmented Forest. University of Chicago Press. Chicago, Illinois.

Harrison, Susan, 1991. Local extinction in a metapopulation context: An empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Hastings, A., and Woling, C.L., 1989. Within-patch dynamics in a metapopulation. Ecology 70:1261-1266.

Hultman, G. Eric, 1978. Trees, Shrubs, and Flowers of the Midwest. Great Lakes Living Press, Chicago. p.77.

Janssens, P., Gullinck, H., 1988. Connectivity, proximity, and contiguity in the landscape interpretation of remote sensing data. Connectivity in Landscape Ecology. Proceedings of the 2nd International Seminar of the International Association of Landscape Ecology p 43-47.

Janzen, D.H., 1983. No park is an island: Increased interference from outside as park size decreases. Oikos 41:402-410.

Johnson, W.C., Sharpe, D.M., DeAngelis, D.L., Fields, E.E., and Olson, R. J., 1981. Modeling seed dispersal and forest island dynamics. p. 215-239.

Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5:173-185.

Kellman, M., 1979. Soil enrichment by neotropical savanna trees. Ecology 67:565-577.

Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V., and Coleman, P.R., 1987. Landscape patterns in a disturbed environment. Oikos 48:321-324.

LaGro Jr., James, 1991. Assessing patch shape in landscape mosaics. Photogrammetric Engineering and Remote Sensing 57:285-293.

Loehle, Craig, and Wein, G., 1994. Landscape habitat diversity: A multiscale information theory approach. Ecological Modeling 73:311-329.

Malcolm, Jay R., 1994. Edge effects in central Amazonian forest fragments. Ecology 75:2438-2445.

McGarigal, Kevin and Marks, B., 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. General Technical Report to Pacific North West -GTR-351. Portland, Oregon: USDA Forest Service, Pacific Northwest Research Station. 122p.

Miles, Donald B., 1994. Introduction to the symposium: Contribution of long-term ecological research to current issues in the conservation of biological diversity. American Zoology 34:367-370.

Noss, R.F., 1983. A regional landscape approach to maintain diversity. BioScience 33:700-706.

Pacala, S.W., 1989. Plant population dynamic theory. In: Perspectives in Ecological Theory. J. Roughgarden, R.M. May, and S.A. Levin eds. Princeton University Press. Princeton, New Jersey p 54-67.

Pearson, Scott M., 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecology 8:3-18.

Pickering M.G., and Gebauer, S.B., 1993. Status report: Assessment of associations between lupine population characteristics and vegetation and soil characteristics - 1991-92. Eastern New York Chapter of the Nature Conservancy. (unpublished).

Ranney, J.W., Bruner, M.C., and Levenson, J.B., 1981. The importance of edge in the structure and dynamics of forest islands. In: Forest Island Dynamics in Man-dominated Landscapes. R.L. Burgess and D.M. Sharpe eds. Springer-Verlag. New York, New York p. 67-95.

Shuey, J.A., Calhoun, J.V., and Iftner, D.C., 1987. Butterflies that are endangered, threatened, and of special concern in Ohio. Ohio Journal of Science 87:98-106.

Shugart, H.H.A., 1984. Theory of forest dynamics: The ecological implications of forest succession models. Springer-Verlag. New York, NY.

Stewart, M.M. and Ricci, C., 1988. Dearth of the blues. Journal of Natural History 92:64-70.

Temple, S.A., and Cary, J.R., 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340-347.

Tester, John R., 1989. Effects of fire frequency on oak savanna in east-central Minnesota. Bulletin of the Torrey Botanical Club 116:134-144.

Thomas, J.W., 1979. Wildlife habitats in managed forests - the Blue Mountains of Oregon and Washington. U.S.D.A. Forest Service Agricultural Handbook. 53 p.

Turner, M.G., Dale, V.H., and Gardner, R.H., 1989. Predicting across scales: Theory development and testing. Landscape Ecology 3:245-252.

Vetaas, O.R., 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science 3:337-344.

Warner, R.R., and Chesson, P.L., 1985. Coexistence mediated by recruitment fluctuations: A field to the storage effect. American Naturalist 125:769-787.

Welch, Robert J., 1993. Dispersal and colonization behavior in the Karner blue butterfly (Lycaeides melissa samuelis) in central Wisconsin. Final Report to U.S. Fish and Wildlife Service 50 p.

Wisconsin Department of Natural Resources Karner Blue Technical Team., 1993. 3rd draft: Wildlife Management Guidelines for Karner blue. (unpublished).

Young, A., 1989. Agroforestry for soil conservation. International Council for Research in Agroforestry. Nairobi, Kenya.

Overall Conclusions

This research provides information about KBB habitat that may prove useful for managers attempting to protect this species. Specifically, light and soil pH appear to affect lupine growth and density. Lupine and KBB distribution, at a landscape level, are affected by forest characteristics and spatial parameters. This provides managers with habitat information at both the individual patch and landscape scales.

The results of our first study indicate that a pH range of 4.2 to 5.6 and the highest available light are associated with highest lupine densities. However, because of the potential for weather extremes such as early summer drought and late spring frost, land managers protecting the KBB should aim to provide lupine habitat that covers a range of canopy, and thus light levels. Such habitat diversity is especially important for an endangered species. Managers need to be cautious and not only provide the best habitat for lupine, but be certain to provide protection against disaster. Managers also need to be concerned with providing these two types of habitat at a spatial scale that biologically benefits KBB. The results of our second study indicate that mean nearest neighbor needs to be less than 70 meters. Thus managers should try to provide both high light and protected areas within 70 meters of each patch of KBB.

To achieve this parameter, managers need not (perhaps should not) focus solely on providing open areas, but instead manage for low to medium density forests. This would provide a continuum of light, litter to maintain a low soil pH, protection from extreme weather conditions, and a timber source. I recommend future research to (1) better define KBB's ecological requirements, and (2) better define a metapopulation model of the KBB.

The broad range of forest density levels under which KBB has been found at ASGA points out the need for a more general definition of oak savanna. Initially, I interpreted oak savanna as openings with very sparsely distributed trees. However, I was surprised to find KBB, (a species that is said to only live in oak savannas, pine barrens, and sand dunes) in high density oak stands. It seemed to me that at ASGA the definition of oak savanna would need to include all stand and density classes, thus broadening the term, which I believe would benefit the KBB by providing protected habitat in many weather conditions.

APPENDICES

APPENDIX A

Proportion of direct light measurement techniques

The camera was aligned with N on a compass by centering the middle of the word Canon on the camera with the N arrow on a compass and the camera was then leveled with the visual aid of a bubble. I laid on the ground below the view of the camera and took the two pictures of the sky. The film was then developed into negatives that I cut and placed into gesepii finger pressure slide cases. I discarded the negative of poorer quality from each plot. In December I traveled to Corvallis Oregon where I used Oregon State University Department of Forestry's equipment and Canopy software of to analyze the slides. Percent sky was determined by taking the ratio of the readings from the actual fisheye image to the clear negative (Chan, et. al, 1986).

APPENDIX B

Table of chemical application history for greenhouse study

Date	Time	Product Name	Active Ingredient	EPA Reg #	Rate	Tot. Amt. Used	Target Pests
02/18/97	4:00 PM	Cleary's 3336-F	Dimethyl 4	4581-352-1001	1 oz/ 5 gal	1 oz	Misc. Fungi
02/18/97	4:00 PM	Subdue	Metalaxyl	100-619	1/4 tsp / 5 gal	1/4 tsp	Pythium
03/25/97	4:30 PM	Aliette	Aluminum tris	264-467	1 tsp / 5 gal	2 tsp	Misc. Fungi
03/25/97	4:30 PM	Captan 50-WP	Captan	10182-145	1 tsp / 5 gal	2 tsp	Misc. Fungi
03/31/97	3:45 PM	Gnatrol	B, thuringiensis	275-52	1 oz / gal	10 oz	Fungus Gnats
04/07/97	4:15 PM	Gnatrol	B, thuringiensis	275-52	1 oz / gal	10 oz	Fungus Gnat Larvae
04/07/97	4:35 PM	Xclude	Pyrethrins	499-239	10 sec / 100 sq ft	5 sec	Fungas Gnat Adults
04/14/97	1:15 PM	Aliette	Aluminum tris	264-467	1 tsp / 5 gal	2 tsp	Misc. Fungi
04/14/97	1:15 PM	Cleary's 3336-F	Dimethyl 4	4581-352-1001	6 tsp / 5 gal	12 tsp	Misc. Fungi
04/14/97	1:15 PM	Gnatrol	B, thuringiensis	275-52	1 oz / gal	10 oz	Fungus Gnats
05/21/97	8:00 AM	Aliette	Aluminum tris	264-467	1 tsp / 5 gal	1.5 tsp	Misc. Fungi
05/21/97	8:00 AM	Cleary's 3336-F	Dimethyl 4	4581-352-1001	6 tsp / 5 gal	9 tsp	Misc. Fungi

BIBLIOGRAPHY

BIBLIOGRAPHY

Alverson, W.S., D.M. Waller, and S.S. Solheim, 1988. Forest too deer: Edge effects in northern Wisconsin. Conservation Biology 2:348-358.

Andersson, T., 1991. Influence of stemflow and throughfall from common oak (Quercus robur) on soil chemistry and vegetation patterns. Canadian Journal of Forest Research 21:917-924.

Bach, C.E., 1988. Effects of host plant patch size on herbivore density: Underlying mechanisms. Ecology 69:1103-1117.

Backs, S.E., and C.H. Eisfelder, 1990. Criteria and guidelines for wild turkey release priorities in Indiana. Proceedings of the National Wild Turkey Symposium. 6:134-143.

Baudry, J., and H.G. Merriam, 1988. Connectivity and connectedness: Functional versus structural patterns in landscapes. Connectivity in Landscape Ecology. Proceedings of the 2nd International Seminar of the International Association of Landscape Ecology p. 23-28.

Belsky, A.J. R.G. Amundson, J. M. Duxbury, S.J. Riha, A.R. Ali, and S.M., Mwonga, 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology 26:1005-1021.

Belsky, A.J., and C.D. Canham, 1994. Forest gaps and isolated savanna trees: An application of patch dynamics in two ecosystems. BioScience 44:77-84.

Bess, J.A., 1989. Status of the Karner blue butterfly, Lycaeides melissa samuelis Nabokov, in the Manistee National Forest. Report to Michigan Natural Features Inventory, Lansing, Michigan 20 p. (unpublished).

Bray, J.R., 1955. The savanna vegetation of Wisconsin and an application of the concepts order and complexity to the field of ecology. Unpublished Ph.D. Dissertation. The University of Wisconsin, Madison. 251 p.

Boyonoski, A.M., 1992. Factors affecting the establishment and maintenance of Lupinus perennis, (wild lupine). M.S. Thesis, University of Guelph, Ontario.

Burgess, Robert L., D. M. Sharpe, and M.C. Bruner, 1981. Forest island dynamics in man-dominated landscapes. Eds. Burgess, R. L. and Sharpe, D. M. New York, Springer-Verlag. 310 p.

Chan, S.S., R.V. McCreight, J.D. Walstad, and T.A. Spies, 1986. Evaluating forest vegetative cover with computerized analysis of fisheye photographs. Forest Science 32:1085-1091.

Clark, J.S., 1991. Disturbance and population structure on the shifting mosaic landscape. Ecology 72:1119-1137.

Clough, M.W., 1992. Endangered and threatened wildlife and plants: Proposed endangered species status for the Karner blue butterfly. Federal Register (January 21, 1991). 57: 2241-2246.

Comins, H.N., and I.R. Noble, 1985. Dispersal, variability, and transient niches: Species coexistence in a uniformly variable environment. American Naturalist 126:706-723.

Cowling, W.A., and J.C. Clements, 1993. Association between collection site soil pH and chlorosis in Lupinus angustifolius industed by a fine-textured, alkaline soil. Australian Journal of Agricultural Research 44:1821-1836.

Crozier, Carl R., and R. E. J. Boerner, 1984. Correlations of understory herb distribution patterns with microhabitats under different tree species in a mixed mesophytic forest. Oecologia 62:337-343.

Curtis, B., 1959. The vegetation of Wisconsin. The university of Wisconsin press. Madison, Wisconsin. 657 pp.

Cryan, J.F., and R. Dirig, 1978. A report on the status of the Karner blue butterfly (Lyceides melissa samuelis Nabokov) in New York State. Report to the U.S. Fish and Wildlife Service.

Dirig, Robert, 1988. Nabokov's blue snowflakes. Natural History 97:68-69.

Edsall, Marian S., 1985. Roadside plants and flowers: A traveler's guide to the Midwest and Great Lakes area: With a few familiar off-road wildflowers. University of Wisconsin Press, Madison Wisconsin.

Ellis, J.E., and J.G. Lewis, 1967. Mobility and annual range of wild turkeys in Missouri. Journal of Wildlife Management 31:568-581.

Forman, R.T.T., and M. Godron, 1986. Landscape Ecology. John Wiley and Sons. New York, New York. 619 p.

Franklin, J.F., and R.T.T. Forman, 1987. Creating landxcape patterns by forest cutting: Ecological consequences and principles. Landscape Ecology 1:5-18

Gilpin, Michael E., 1987. Metapopulation structure and population vulnerability. In: Viable populations for conservation. Cambridge University Press. New York, New York p. 125-139.

Givnish, T.J., E.S. Mengis, and D.F. Schweitzer, 1988. Minimum area requirements for long-term conservation of the Albany Pine Bush and Karner blue butterfly: An assessment. (unpublished).

Gustafson, Eric J., G.R. Parker, and S.E. Backs, 1994. Evaluating spatial pattern of wildlife habitat: A case study of the wild turkey (Meleagris gallopavo). Midland Naturalist 131:24-33.

Haack, R.A., 1993. The endangered Karner blue butterfly (Lepidoptera: Lycaenidae): Biology, management considerations, and data gaps. Proceedings of the 9th Central Hardwood Forest Conference. U.S.D.A. -Forest Service, North Central Forest Experiment Station. St. Paul, Minnesota. p. 83-100.

Harris, L.D., 1984. The Fragmented Forest. University of Chicago Press. Chicago, Illinois.

Harrison, Susan, 1991. Local extinction in a metapopulation context: An empirical evaluation. Journal of the Linnean Society 42:73-88.

Hastings, A., and C.L. Woling., 1989. Within-patch dynamics in a metapopulation. Ecology 70:1261-1266.

Herms, Catherine P., 1996. The endangered Karner blue butterfly (Lepidoptera: Lycaenidae) in Michigan: Habitat suitability, potential impacts of gyspy moth (Lepidoptera: Lymantriidae) suppression and labortory rearing. Unpublished Masters Thesis, Department of Entomology, Michigan State University.

Holland,V.L., 1973. A study of soil and vegetation under Quercus douglasii compared to open grassland. Unpulbished PhD. Dissertation, Department of Botany, University of California, Berkeley. 359 p.

Hultman, G. Eric, Trees, Shrubs, and Flowers of the Midwest. 1978. Great Lakes Living Press, Chicago. p.77.

Janssens, P., and H. Gullinck, 1988. Connectivity, proximity, and contiguity in the landscape interpretation of remote sensing data. Connectivity in Landscape Ecology. Proceedings of the 2nd International Seminar of the International Association of Landscape Ecology. p. 43-47.

Janzen, D.H., 1983. No park is an island: increased interference from outside as park size decreases.. Oikos. 41:402-410.

Johnson, W.C., D.M. Sharpe, D.L. DeAngelis, E.E. Fields, and R. J. Olson. 1981. Modeling seed dispersal and forest island dynamics. p. 215-239.

Kapos, V., 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology 5:173-185.

Kellman, M., 1979. Soil enrichment by neotropical savanna trees. Ecology 67:565-577.

Krummel, J.R., R.H. Gardner, G. Sugihara, R.V. O'Neill, and P.R. Coleman, 1987. Landscape patterns in a disturbed environment. Oikos 48:321-324.

LaGro Jr., James, 1991. Assessing patch shape in landscape mosaics. Photogrammetric Engineering and Remote Sensing 57:285-293.

Loehle, Craig, and G. Wein, 1994. Landscape habitat diversity: A multiscale information theory approach. Ecological Modeling 73:311-329.

Malcolm, Jay R., 1994. Edge effects in central Amazonian forest fragments. Ecology 75:2438-2445.

Maxwell, J., and T. Givnish, 1993. Research on the Karner blue butterfly at Fort McCoy, Wisconsin: Progress report for the 1993 field station. Report submitted to the US Fish and Wildlife Service, and the Department of the Army. (unpublished).

McGarigal, Kevin, and B. Marks, 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. General Technical Report Pacific North West-GTR-351. Potland, Oregon: U.S.D.A. - Forest Service, Pacific Northwest Research Station. 122 p.

Miles, Donald B., 1994. Introduction to the symposium: Contribution of long-term ecological research to current issues in the conservation of biological diversity. American Zoology 34:367-370.

Miller, Ellen, and M. C. Whiting, 1895. Wildflowers of the North-Eastern states. G.P. Putnam's Sons. The Knickerbocker Press, New York.

Noss, R.F., 1983. A regional landscape approach to maintain diversity. BioScience. 33:700-706.

Opler, P.A., and G.O. Krizek, 1984. Butterflies East of the Great Plains. John Hopkins University Press, Baltimore, Maryland. p. 120-121.

Pacala, S.W., 1989. Plant population dynamic theory. In: Perspectives in ecological theory. J. Roughgarden, R.M. May, and S.A. Levin eds. Princeton University Press. Princeton, New Jersey. p. 54-67.

Parker, V.T., and C.H. Muller, 1982. Vegetation and environmental changes beneath isolated live oak trees (Quercus Agrifolia) in a California Annual Grassland. American Midland Naturalist 107:69-81.

Pearson, Scott M., 1993. The spatial extent and relative influence of landscape-level factors on wintering bird poulations. Landscape Ecology 8:3-18.

Pickering M.G., and S.B. Gebauer, 1993. Status report: Assessment of associations between lupine population characteristics and vegetation and soil characteristics - 1991-92. Eastern New York Chapter of the Nature Conservancy. (unpublished).

Ranney, J.W., M.C. Bruner, and J.B. Levenson, 1981. The importance of edge in the structure and dynamics of forest islands. p. 67-95.

Rich, P.M., 1989. A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory. Los Alamos, New Mexico. 80 p.

Scudder, S.H., 1889. The Butterflies of Eastern United States and Canada with special reference to new England. Cambridge, Massachucetes. p. 964-969.

Shuey, J.A., J.V. Calhoun, and D.C. Iftner, 1987. Butterflies that are endangered, threatened, and of special concern in Ohio. Ohio Journal of Science 87:98-106.

Shugart, H.H.A., 1984. Theory of forest dynamics: The ecological implications of forest succession models. Springer-Verlag. New York, New York.

Smallidge, P.J., and D.J. Leopold, 1992. Environmental factors and critical habitat for Lycaeides melissa samuelis along transmission line rights-of-way in east-central New York, USA. (Draft).

Smith, Helen Vandervort, 1966. Michigan Wildflowers. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Spies, T.A., W.S. Ripple, and G.A. Bradshaw, 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555-568.

Stewart, M.M., and C. Ricci, 1988. Dearth of the blues. Journal of Natural History 92: 64-70.

Tang, Caixian, J. Kuo, N.E. Longnecker, C.J. Thompson, and A.D. Robson, 1992. High pH causes disintegration of the root surface in Lupinus angustifolius L. Annals of Botany 71:201-207.

Tang, Caixian, and A.D. Robson, 1993. pH above 6.0 reduces nodulation in Lupinus species. Plant and Soil. 152:269-276.

Temple, S.A., and J.R. Cary, 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. Conservation Biology 2:340-347.

Tester, John R., 1989. Effects of fire frequency on oak savanna in east-central Minnesota. Bulletin of the Torrey Botanical Club 116:134-144.

Thomas, J.W., 1979. Wildlife habitats in managed forests - the Blue Mountains of Oregon and Washington. U.S.D.A. - Forest Service Agricultural Handbook. 53 p.

Thomson, James, D. G. Weiblen, B.A. Thomas, S. Alfaro, and P. Legendre, 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. Ecology 77:1698-1715.

Turner, M.G., V.H. Dale, and R.H. Gardner, 1989. Predicting across scales: Theory development and testing. Landscape Ecology 3:245-252.

Vetaas, O.R., 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science 3:337-344.

Warner, R.R.,and P.L. Chesson, 1985. Coexistence mediated by recruitment fluctuations: A field to the storage effect. American Naturalist 125:769-787.

Welch, Robert J., 1993. Dispersal and colonization behavior in the Karner blue butterfly (Lycaeides melissa samuelis) in central Wisconsin. Final Report to U.S. Fish and Wildlife Service 50 p.

Wisconsin Department of Natural Resources Karner Blue Technical Team., 1993. 3rd draft: Wildlife Management Guidelines for Karner blue. (unpublished).

Young, A., 1989. Agroforestry for soil conservation. International Council for Research in Agroforestry. Nairobi, Kenya.

Zinke, P.J., 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43:130-133.