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I am submitting herewith a dissertation written by Maureen Cunningham entitled "Population Biology of a Rare Hemiparasite, *Aureolaria patula* (Chapman) Pennell (Scrophulariaceae): Demographic Trends, Host Interactions and Reproductive Biology." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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POPULATION BIOLOGY OF A RARE HEMIPARASITE, *AUREOLARIA PATULA* (CHAPMAN) PENNELL (SCROPHULARIACEAE): DEMOGRAPHIC TRENDS, HOST INTERACTIONS, AND REPRODUCTIVE BIOLOGY

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Maureen Cunningham

May 2000

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DEDICATION

This work is dedicated to my husband, Webb Van Winkle, whose tireless efforts and abundant support made this endeavor manageable, and to my parents, Eileen B. Cunningham (now deceased) and James W. Cunningham, for nurturing a love of learning.

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Many friends and family members helped with the extensive field work required for the demographic study, especially: Webb Van Winkle, Clare Cunningham, Krista McKinney, Laura Heiser, and Jim Cunningham. Ken Swain loaned a trawling motor for my canoe, which made travel to and from field sites considerably easier and faster.

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ABSTRACT

Aureolaria patula, spreading false-foxglove, is a rare herbaceous perennial restricted to calcareous slopes and bluffs along waterways in Alabama, Georgia, Kentucky, and Tennessee, primarily along the Tennessee River and its tributaries. *Aureolaria patula* is a root hemiparasite. It has green stems and leaves and functional chlorophyll, but it attaches via haustoria to the roots of host trees to access water and solutes in the vascular system of the host.

I measured individual and population growth characteristics of four populations on public lands in east Tennessee and evaluated demographic structure and processes using a stage-based matrix projection model. Plants were found to have the ability to be dormant for a growing season, then return the following year. Probability of dormancy and mortality decreased with increasing plant size. Reproductive effort increased with increasing plant size. Dormant stages were incorporated in the population model and were shown to be important influences on population growth rate (λ) at some sites. Population growth rates varied both spatially and temporally and ranged from 0.35 to 1.6. The relative importance of fecundity, growth, and survival in the dynamics of the populations varied by site and year. Survival of larger plants had the greatest influence on λ at undisturbed, level sites, while fecundity and growth of a mix of size classes were important at sites on moderate slopes (15-18%). Characterization of demographic monitoring sites revealed that *Ostrya virginiana, Carpinus carolinana*, and *Quercus rubra* dominated the canopy vegetation. All sites had moderate to high levels of phosphorus in the soil.

Studies of plant growth in containers in a greenhouse showed host tree had a significant effect on shoot and root biomass of *A. patula* and *A. virginica*, a common relative. The most beneficial hosts for *A. patula* were *Carpinus carolinana, Quercus rubra*, and *Cornus florida*. Hosts promoting the greatest growth of *A. virginica* were *Carpinus*

most beneficial hosts for *A. patula* were *Carpinus caroliniana, Quercus rubra,* and *Cornus florida.* Hosts promoting the greatest growth of *A. virginica* were *Carpinus caroliniana, Cercis canadensis,* and *Cornus florida. Aureolaria patula* grew larger than *A. virginica* on all hosts and grew as well as *A. virginica* without a host in nutrient-poor soil. Number of haustoria was positively correlated with shoot biomass of the hemiparasites. Although the two hemiparasites formed haustoria on most host trees tested, some host species were clearly more beneficial than others to the hemiparasites. The attachment to a host, however, was not without risk. The results of two experiments indicate evidence of harm to the hemiparasite when growing with or attached to some hosts. Survival of hemiparasite seedlings was significantly affected by host species, and growth of shoots and roots of both hemiparasites was significantly suppressed by the presence of *Cercis canadensis.* Both hemiparasites grew larger and formed more haustoria on the host when fertilized.

An investigation of reproductive biology in a small population revealed that *A. patula* is self-incompatible. Seedlings from open-pollinated flowers on seven maternal plants grew significantly larger in a greenhouse than seedlings from flowers hand-outcrossed with plants 30-m distant. There was no evidence of inbreeding depression in seedling growth in the small population studied.

Aureolaria patula can be viewed as having a more opportunistic life history strategy than *A. virginica,* which has the strategy of a generalist. The conditions under which *A. patula* thrives include plant communities with a high density of the most beneficial hosts, lack of herbaceous competitors that block light, proximity to a river or stream, and calcareous substrate. Environmental conditions 9,000 years before present may have favored the most beneficial hosts of *A. patula* in the region of its current distribution. Today *A. patula* remains geographically restricted because its favored habitat is patchy, and because self-incompatibility makes colonization of new sites by long distance seed dispersal less probable.

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Chapter 1. General Introduction

Theoretical and practical considerations fuel the interest of biologists in rare species. The study of rare species may provide clues to fundamental principles of distribution and abundance relevant for all species (Carter and Prince 1987). In addition, conservation efforts for an increasing number of rare species call for detailed information on life history, demographic trends, and important interactions with other organisms and the landscape (Schemske 1994). For many rare species, little biological or ecological information is available to help with these efforts. This study focuses on temporal and spatial variation in demography, crucial interactions with other species, reproductive biology, and offspring vigor of a rare plant species, *Aureolaria patula* (Chap.) Pennell (Scrophulariaceae). Observation of field populations throughout the seasons enables a more complete view of life history of a species, as well as the role of environmental stochasticity in population dynamics. I chose *A. patula* as a species for study because almost no information is available on its life history and because several populations were accessible for study throughout the year. Studies on important demographic and reproductive processes in populations of a rare species and variability in these processes over time and space may yield information relevant to conservation-related questions and actions for other rare plant species.

Aureolaria patula, spreading false foxglove, is a rare perennial whose known geographic range is restricted to the corridors of several rivers and streams in Tennessee, Kentucky, northern Georgia, and northern Alabama (Kral 1983) (Fig. 1.1). It was listed as a candidate species (Category 2) by the U.S. Fish and Wildlife Service (FWS) under the Endangered Species Act of 1973, as amended (U. S. Fish and Wildlife Service 1985). This designation meant there was evidence that the species was rare and potentially threatened, but the FWS lacked sufficient information to determine if listing as threatened or endangered were warranted (U. S. Fish and Wildlife Service 1985). In a 1996 decision published in the Federal Register the FWS eliminated Category 2 candidate species from its lists, retaining only Category 1 species that are expected to be

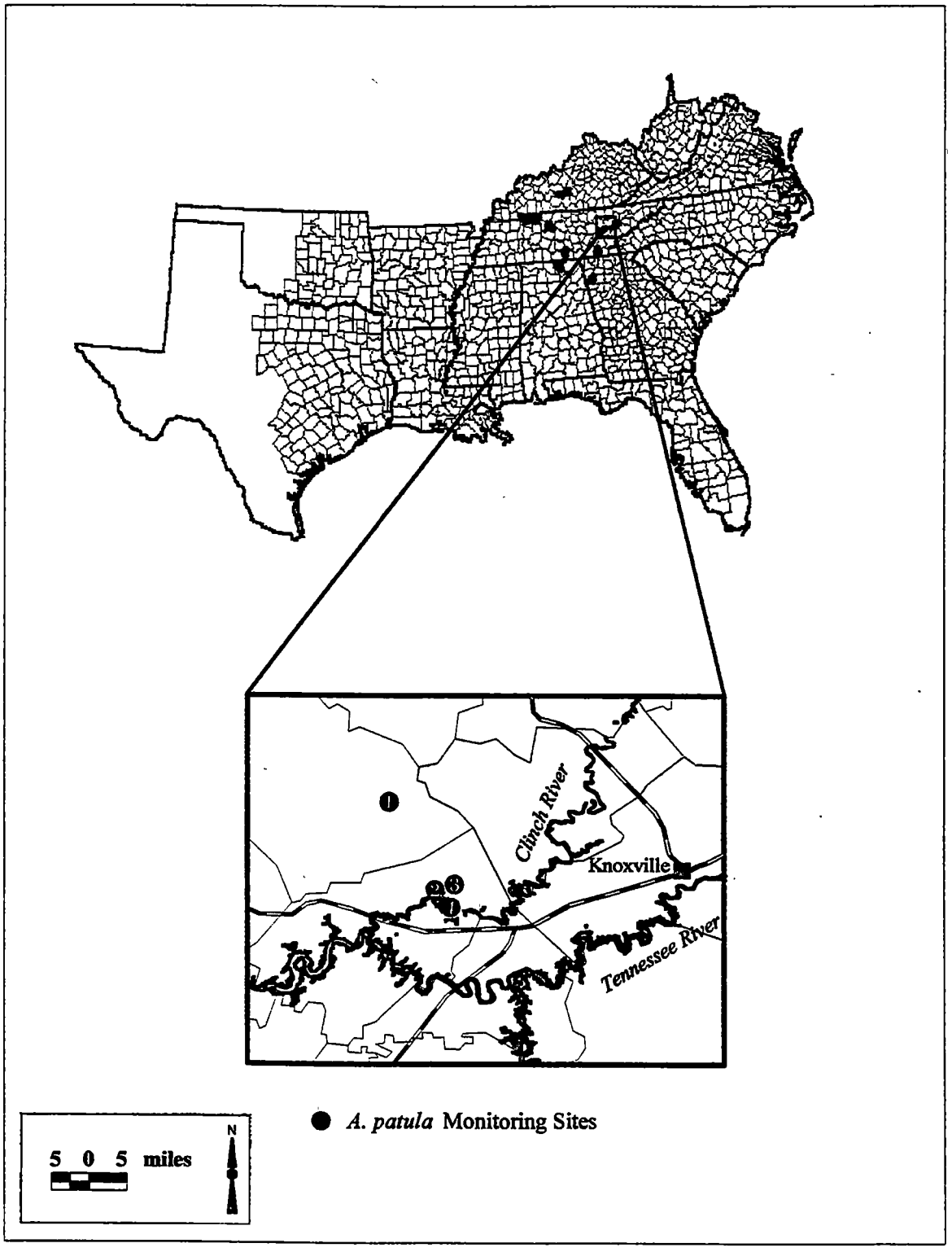


Fig. 1.1. Distribution of *A. patula* by county of occurrence in Alabama, Georgia, Kentucky, and Tennessee with blowup showing the four demographic monitoring sites.

proposed for listing (61 FR 64481). The State of Tennessee lists *A. patula* as threatened within the state (Tennessee Department of Conservation 1998); Kentucky, Georgia and Alabama list it as a species of special concern (Kentucky State Nature Preserves Commission 1999; Georgia Natural Heritage Program 1999; Alabama Natural Heritage Program 1996). State Natural Heritage Programs, in consultation with The Nature Conservancy, assign global ranks (G1 (greatest rarity)-G5) to indicate rarity throughout the species' range, without regard to political boundaries (Tennessee Department of Conservation 1998). All states in which *A. patula* occur have assigned a global rank of G2 (imperiled globally) (Tennessee Department of Conservation 1998; Kentucky State Nature Preserves Commission 1999; Georgia Natural Heritage Program 1999; Alabama Natural Heritage Program 1996).

Pennell (1935,1928) included *A. patula* in his studies of the Scrophulariaceae and provided a description of morphology, putative hosts, pollinators and presumed relationship to other species in the genus. *Aureolaria patula* is a herbaceous perennial that reproduces exclusively by seed. Plants emerge early in the spring from perenniating buds just below the ground surface. Stems begin elongating in late spring. By August when flowering occurs, stems number from one to 50 per plant and may reach up to two meters in length. Longer stems are usually arched and spreading rather than upright. Stems are brittle; they are easily broken by passing animals and fallen tree limbs. Stems are frequently grazed by deer, particularly plants away from the river edge where deer have a more stable footing. Browsed stems typically develop side branches from axillary buds and may subsequently flower and set fruit. Insect larvae and pupae are sometimes present in fruits but have not been successfully identified. It is not uncommon for stems to turn brown and die prior to fruiting due to damage from insects that bore into the base of stems.

The large tubular yellow flowers of *A. patula* are arranged in opposite pairs on the terminal portions of stems and side branches in late August and September (Fig. 1.2). A single large stem may have up to 100 flowers, but typically the number is less.



Fig. 1.2 Yellow tubular flowers of *A. patula* are present in August and September.

Bumblebees are considered the primary pollinators (Pennell 1935, 1928), and my field observations support this. Seeds mature and are shed in late fall. They are relatively small (1.5- to 2.5-mm long) and covered with reticulations, as has been described for several other species of *Aureolaria* (Musselman and Mann 1976). The morphology indicates no specialization for particular modes of dispersal, though the reticulations may increase surface area for movement by wind (Pennell 1935). Kuijt (1969) has suggested that reticula are adaptations for water dispersal by trapping air and aiding in buoyancy. Seeds germinate in the spring, presumably following the fall season in which they were dispersed. There is no published information on the longevity of *A. patula* seed in the soil. Growth of the seedlings, which form rosettes in the first year of growth, is relatively slow. Presumably seedlings in the wild must attach to the roots of a suitable host for significant growth to occur. Seedlings are discernable in the field in midsummer after germination.

The distribution of *Aureolaria patula* is habitat specific within its narrow geographic range (Kral 1983). The typical habitat is limestone ledges, slopes, and bluffs along certain waterways, namely the Tennessee River along with some of its tributaries and the Green River in Kentucky. *Aureolaria patula* is most abundant at edge locations - at forest edges along rivers or along trails or roads near the rivers. Restriction to slopes along waterways suggests that microclimatic or landscape-level dispersal features of the habitat may be important. Temperatures would be expected to be cooler near waterways, and free-flowing rivers and streams can transport and deposit seeds effectively. Alternatively the habitat preferences of *A. patula* in terms of edaphic features may be present mainly along waterways, where erosional processes have exposed limestone slopes.

A special report to the U.S. Forest Service on rare species of the southeastern U.S.A. (Kral 1983) indicates that the habitat of *A. patula* is considered at risk due to shoreline development. Although the Tennessee Valley Authority (TVA) Heritage Program has surveyed much of the TVA region for occurrence of *A. patula* and has documented

occurrences in their data base (J. L. Collins, TVA, personal communication), little is known of the specifics of its life history and population biology. The construction of dams and creation of reservoirs on rivers where *A. patula* grows has eliminated some of its former habitat and altered the remaining habitat. Whether these alterations have on balance negatively or positively affected populations of *A. patula* is unknown.

The assessment of threat to *A. patula* and appropriate conservation efforts are complicated by the fact that it is a root hemiparasite (Kral 1983; Pennell 1928). It attaches to the roots of tree species by forming haustoria (specialized enlarged root structures (Kuijt 1969)) that penetrate the vascular tissue of the host. Hemiparasitism is not uncommon in the Scrophulariaceae; about one-third of the species in the family have this capability (Kuijt 1969). However, the various species differ in their requirement for a host and in their host specificity (see Watkinson and Gibson 1988 for review). One obvious question to ask about a rare hemiparasite is whether the relationship with its hosts plays a major role in its rarity. In a review of conservation considerations for rare plant parasites, Marvier and Smith (1997) indicate "...few studies have addressed the extent to which parasitic plant populations are limited by the availability of hosts...it is often not clear what the preferred hosts are for parasitic plants nor how much specialization exists." The present study is designed in part to test alternative hypotheses concerning host usage and suitability of different hosts for *A. patula* compared to *A. virginica*, a commonly occurring congener.

The objectives of my research are: 1) to increase knowledge of the life history of *A. patula*, including the demographic structure of populations and the demographic processes crucial to population persistence; 2) to investigate the range of host species and the relative benefit of different host species for *A. patula* and *A. virginica*; and 3) to explore how the relationship between demographic processes, host-interactions, and reproductive biology might define the occurrence of *A. patula* on the regional landscape.

Chapter 2. Demographic Study of *Aureolaria patula* in East Tennessee

2.1 Introduction

Schemske et al. (1994) reviewed current approaches to conservation of rare and endangered species. The authors concluded that most of the reports "are of limited use in an initial assessment of species status because they cannot predict population vital rates or the future viability of populations," i.e., they do not indicate whether the population size is increasing, decreasing or remaining stable. Neither do they indicate which life stages are the most sensitive and function as a bottleneck to population growth and species persistence. Finally, they do not address the biological causes of variation in the most sensitive life stages. Demographic studies are more appropriate because they track the age or size distribution of individuals in the population over time, as well as the reproductive potential of the population. These studies allow evaluation of demographic trends as well as variability in these trends over space and time.

Since the review by Schemske et al. (1994) studies of demographic trends and spatiotemporal variation in demographic pattern have been reported for a range of species with differing life histories (Morris and Doak 1998; Valverde and Silvertown 1998; Horvitz and Schemske 1995). These reports involving application of population models to plant species encourages the use of models for rare species conservation efforts (Silvertown et al. 1996).

Several investigators have used quantitative tools for demographic analysis successfully, particularly the matrix projection model, in studies of rare or vulnerable plant species. Nault and Gagnon (1993) described demographic trends and critical life stages for population stability in ramp, *Allium tricoccum*, at the northern limits of its distribution in southern Quebec. The authors were able to show that undisturbed populations were stable; however, simulated harvesting rates of only 5-15% were sufficient to reduce population growth rates so that a population decline was projected.

Menges (1990) reported on the distribution, demographic trends, and projected population viability for the endemic lousewort, *Pedicularis furbishii*. Menges was able to show that loss of entire populations by bank scour was the most serious threat to the species. Preserving only extant populations would not be a successful conservation strategy for this species; suitable "empty" sites for establishment of new populations should be components of a preserve system to protect *P. furbishii*.

Menges and Dolan (1998) compared demographic trends in 16 populations of *Silene regia*, a rare perennial of midwestern prairies. They found that the importance of certain life stages to population persistence varied spatially and according to site management. Higher growth rate and higher fecundity were found to be more crucial in populations subject to periodic burning, but at unburned sites survival of adult stages was most important in population persistence. Byers and Meagher (1997) used a matrix projection model to compare demographic trends in populations of a rare and a common *Eupatorium*. *Eupatorium resinosum*, the rare species, produced fewer new individuals through seedlings and ramets, but survivorship of new individuals was higher than for *E. perfoliatum*, the common species. Survivorship of nonflowering individuals was found to be crucial to population maintenance in *E. resinosum*, while survivorship of flowering individuals was more important for populations of *E. perfoliatum*. Kephart and Paladino (1997) looked at patterns in demographic parameters of *Silene douglasii var. oraria*, a coastal grassland endemic, in grassy and rocky microhabitats. They found that local scale variability in sites influenced demographic characteristics; lower adult plant mortality and greater recruitment of juveniles occurred in rocky sites.

Plant dormancy has been reported for several rare perennial species (e.g., Kephart & Paladino 1997; Lesica and Steele 1994; Mehroff 1989b; Hutchings 1987). Menges and Dolan (1998) encountered plant dormancy in their study of *Silene regia*, but considered it a minor component of population dynamics that seemed reasonable to ignore in their population model. Orchids have been reported to go dormant for multiple years (Mehroff 1989a, 1989b), and investigators conducting a long-term (10-yr) study of the

rare orchid, *Isotria medeoloides*, in Maine have calculated a probability of reemergence based on empirical data (Pati Vitt, University of Conn. and Chicago Botanic Garden, personal communication). No inferred dormancies were included in their calculation; a plant had to be tagged, disappear and then reappear to be included in the probability of reemergence calculation. Their data showed frequency of reemergence dropped as length of dormancy increased. In a long-term study of the early spider orchid, *Ophrys sphegodes*, Hutchings (1987) found a similar pattern, with the greatest observed dormancy being five years. Mehroff (1989b) reported a maximum dormancy period of three years for *Isotria medeoloides*.

The problems presented by plant dormancy in a demographic study are two-fold. First, determining stage-specific abundance at any point in time becomes more uncertain when plants can remain viable but have no above-ground presence for a season or more (Lesica and Steele 1994). Second, the inability to account for the source or fate of some plants from one census to the next increases the uncertainty in estimates of recruitment and mortality. If dormancy is an important component of population demography, studies of individually marked plants for multiple years can document the frequency of occurrence and the average duration of dormancy.

The present study was undertaken to characterize life history and demographic patterns of *A. patula* across sites (populations) and years. Specifically, I asked these questions: 1) What is the demographic structure of populations? 2) How do growth, survival, and reproduction differ by plant size? 3) Does plant dormancy occur, and if so, what is the typical duration? 4) Is there spatial and temporal variability in demographic variables? and 5) What are the life stages most crucial to population dynamics?

2.2 Field Sites

Demographic studies were conducted on populations of *A. patula* at four sites located on publicly-owned land. Three of the four sites have limited public access; they are located on or adjacent to the Department of Energy's Oak Ridge Reservation in

Anderson and Roane counties at Oak Ridge, TN (Fig. 2.1). The fourth population is located at Frozen Head State Park in Morgan County, near Wartburg, TN (Fig. 2.2). The sites were selected to represent the range of conditions under which *A. patula* grows in east Tennessee, as well as relative ease of access and freedom from human disturbance during the course of the study. The sites at Oak Ridge are all in close proximity to the Clinch River or its tributaries below Melton Hill Dam and are part of the Watts Bar (WB) impoundment. A detailed description of each site is given in Appendix 1. A brief summary here will give an indication of the general environmental conditions at the sites. The Grassy Creek (GC) site is a heavily wooded northwest-facing steep slope with calcareous rock outcrops; it is located along the Grassy Creek embayment of WB. The Filtration Pond (FP) site, located adjacent to a spring-fed pond that empties into WB, is level to sloping, wooded, and without rock outcrop. The Clinch River site (CR) is along the main channel of the former Clinch River, on a moderately steep, southwest-facing slope with shallow soils and abundant rock outcrop. Measurements of half the plants at CR had to be made standing in a canoe because of a high, deeply undercut and sloughing riverbank. The Frozen Head site (FZ) is on relatively deep sandstone-derived soils along Flat Fork Creek, a tributary of the Emory River, which empties into WB.

2.3 Field Study Methods

2.3.1 Population Sampling

Delimiting a population of *A. patula* is problematic because groups of individuals typically occur in linear corridors along waterways, with natural breaks of varying extent in the distribution of plants. At FP all plants in the small population were included in the demographic study. At the other three sites the census areas were delimited based on natural breaks in plant occurrence and manageability of study components, such as seedling census. Areas censused were approximately 9 x 25 m, and population sizes ranged from 60 to 340 plants. In the late summer of 1995 all plants in the study areas were assigned an identification number and labeled with an aluminum tag held in place with a nail inserted into the soil at the base of each plant.

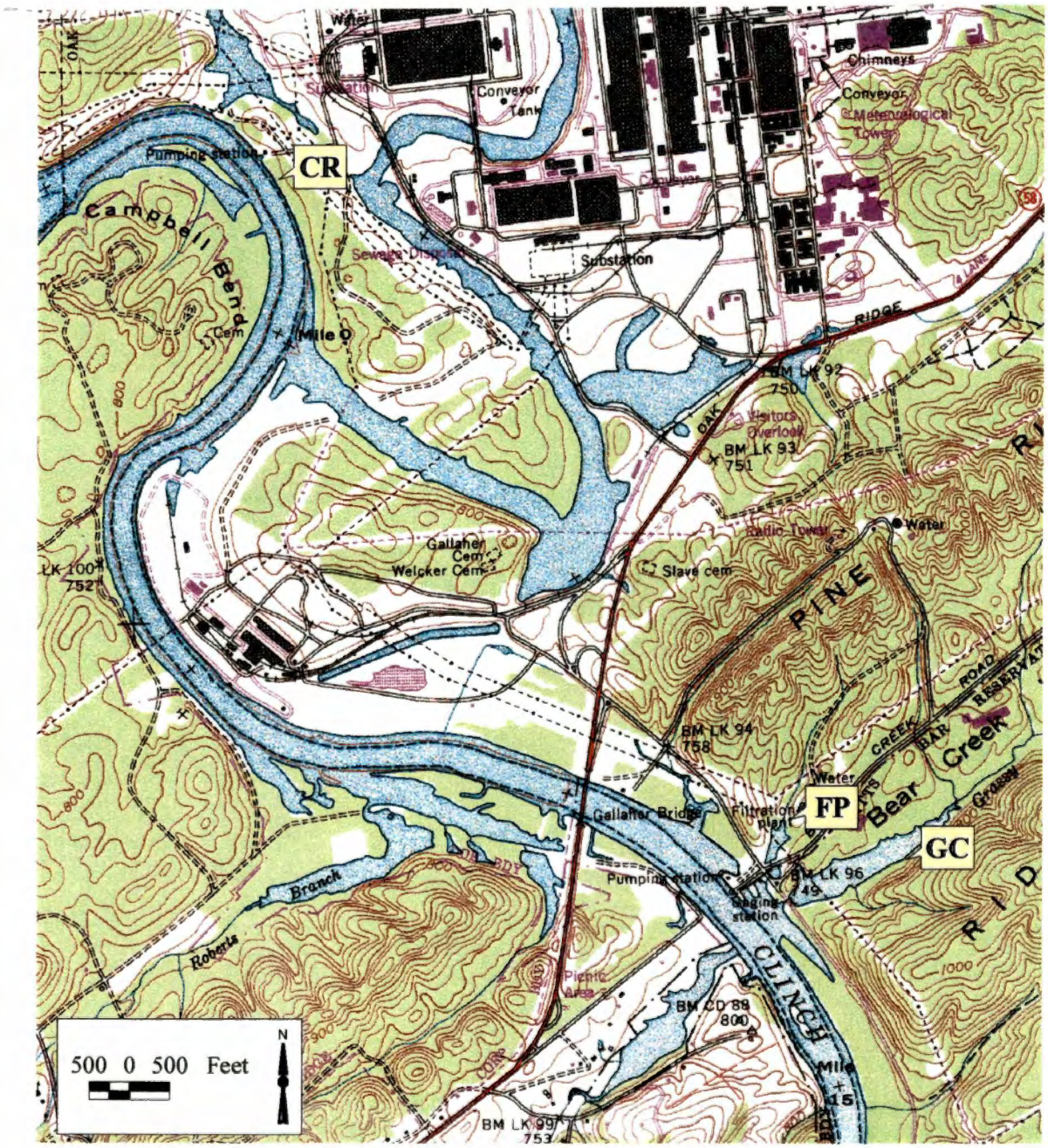


Fig. 2.1 Location of three sites for demographic monitoring of *A. patula* during 1995-1998. The Clinch River site (CR) (N 35° 55'83"-W 84° 24'58") and the Filtration Pond site (FP) (N 35° 54'6"-W 84° 23'47") are within the DOE Oak Ridge Reservation. The Grassy Creek site (GC) (N 35° 54'50"-W 84° 23'05") is located on adjoining land owned by the Tennessee Valley Authority. (From Elverton, TN, USGS 7.5 min Topographic Map)



Fig. 2.2 Location of fourth site for demographic monitoring of *A. patula* during 1995-1998 at Frozen Head State Park (FZ) (N 36° 7'84"-W 84° 29'95") near Wartburg, Tennessee. The monitoring site is along Flat Fork Creek just within the Park boundary. (From Corbin, KY;TN, USGS 15 min Topographic Map)

Location of tagged individuals was mapped in relation to two permanent reference pins (steel reinforcing bar driven into the ground at least six inches) at each site.

Indices of plant size (e.g., leaf area or stem diameter) and reproductive effort (e.g., infloresence length, number of flowers or fruits) are typically used in demographic studies to group individuals for analysis (Menges and Dolan 1998; Morris and Doak 1998; Valverde and Silvertown 1998; Horvitz and Schemske 1995; Menges 1990). *Aureolaria patula* plants can have multiple stems of varying diameters. To estimate plant sizes, I recorded the number of stems and basal diameters of the five largest stems per plant in August. Reproductive effort was estimated in October by counting the number of fruits on up to five randomly chosen stems per plant. Twenty fruits were selected at random in the population and the number of seeds per fruit was determined. These measurements were made on all individuals above ground in late summer or fall 1995, 1996 and 1997. Size measurements were made in early summer 1998; no fruiting measurements were made in 1998.

2.3.2 Field Site Characteristics

Selected biotic and abiotic characteristics of each field site were evaluated. Dominant canopy vegetation was determined by measuring frequency and diameter of all trees ≥4 cm dbh. Species importance in the community was calculated as the sum of relative density and relative basal area (relative dbh). Soil properties (pH, textural classification, macronutrient status, cation exchange capacity, and percent cation saturation) were determined by a commercial laboratory (A&L Analytical Laboratories, Inc., Memphis TN) from composite soil samples. Slope, aspect, and soil depth were determined in the field.

2.4 Field Study Results

2.4.1 Population Sampling

Field data for individual plants at each of the four sites for each of the four years is presented in Appendix 2. The number of stems, basal area (defined as product of number of stems and average stem diameter), and number of fruits produced by five

randomly chosen stems are given for each plant. From one year to the next, plants were found to be capable of growth to a larger size, remaining the same size, regression to a smaller size, or dormancy. I found no evidence of vegetative reproduction; individual plants are separate from each other but occasionally grow closely enough to require delineation with flagging tape for consistency in stem counts from year to year.

Plant dormancy was a common annual occurrence at CR but was less common at the other sites. At FP 100% of the plants became dormant in 1997 after dramatic changes in soil moisture level associated with flooding from a beaver dam. Probability of being dormant in a given year was related to plant size in the previous year. Excluding the FP site for year 1997, when no plants were visible, my data show a decreasing probability of entering dormancy for larger size classes (26 % for nonreproductive plants, 17 % for small adult plants (6.1-15.0 basal area), 9% for medium adult plants (15.1-56.0 basal area), and 3% for large adult plants (>56.0 basal area)). The probability of reemergence from dormancy was related to size; the larger plants had a greater chance of reemerging from dormancy than the smaller plants (21, 33, 61, and 67 % of dormant plants for nonreproductive, small, medium and large adult plants, respectively).

The number of dormant plants ranged from 4 to 36 % of the population (excluding seedlings) for the 12 site-by-year combinations. The typical length of dormancy was one year. For calculation of dormancy duration I considered only plants that plants were tagged, went dormant, then reemerged from dormancy during my years of monitoring. Pooling over all years and populations (except FP in 1997, when no plants were visible), I found that 30 plants were dormant for one year, but only one plant remained dormant for two years before reemerging. The actual number of plants exhibiting dormancy was undoubtedly considerably more; these 31 plants were cases of observed rather than inferred dormancy. Dormancy was inferred if a new adult plant appeared in the population.

The number of fruits produced by each plant was positively correlated with basal area. As an example, the relationship between these two variables is illustrated for the Frozen Head site (Fig. 2.3) ($N = 190$; Pearson's coefficient, $r = 0.68$; $P < 0.01$). The data points in Fig. 2.3 showing no fruit production by plants larger than 15.1 basal area are primarily due to heavy grazing by deer, insect damage to stems, or stem breakage from fallen branches during windstorms.

2.4.2 Field Site Characteristics

Tree species present at each field site and their relative density, relative basal area, and importance value are given in Appendix 1. Three species had high importance values at all four sites: *Carpinus caroliniana* (ironwood), *Ostrya virginiana* (hop hornbeam), and *Quercus rubra* (red oak). Slopes and aspect were variable among sites, ranging from almost level to moderately steep slopes (15-20%) with either northwestern or southwestern aspects. Average soil depth varied from 11 to 12 cm at CR and GC to greater than 23 cm at FP and FZ. Soils were acidic at all sites, notably so at FZ, FP, and GC (pH = 3.1, 4.1, and 4.1, respectively) and less so at CR (pH = 6.5). The analysis of soil mineral elements showed no consistent pattern except for phosphorus, which was at medium to very high levels at all sites.

2.5 Population Model

2.5.1 Stage Categories

To analyze the dynamics of *A. patula* at the four sites, I used the standard stage-based population projection model (Caswell 1989). The model is based on classifying individual plants into stage categories that are determined from size and other relevant characteristics of the species' life cycle. Individuals grouped together in a stage are expected to share common demographic characteristics (Valverde and Silvertown 1998; Byers and Meagher 1997; Horvitz and Schemske 1995; Charron and Gagnon 1991; Fiedler 1987). In defining stage categories it is important to not define stages so narrowly that the number of individuals in each stage may be so small as to result in sampling errors. It is equally important to not define stages so broadly that the smallest

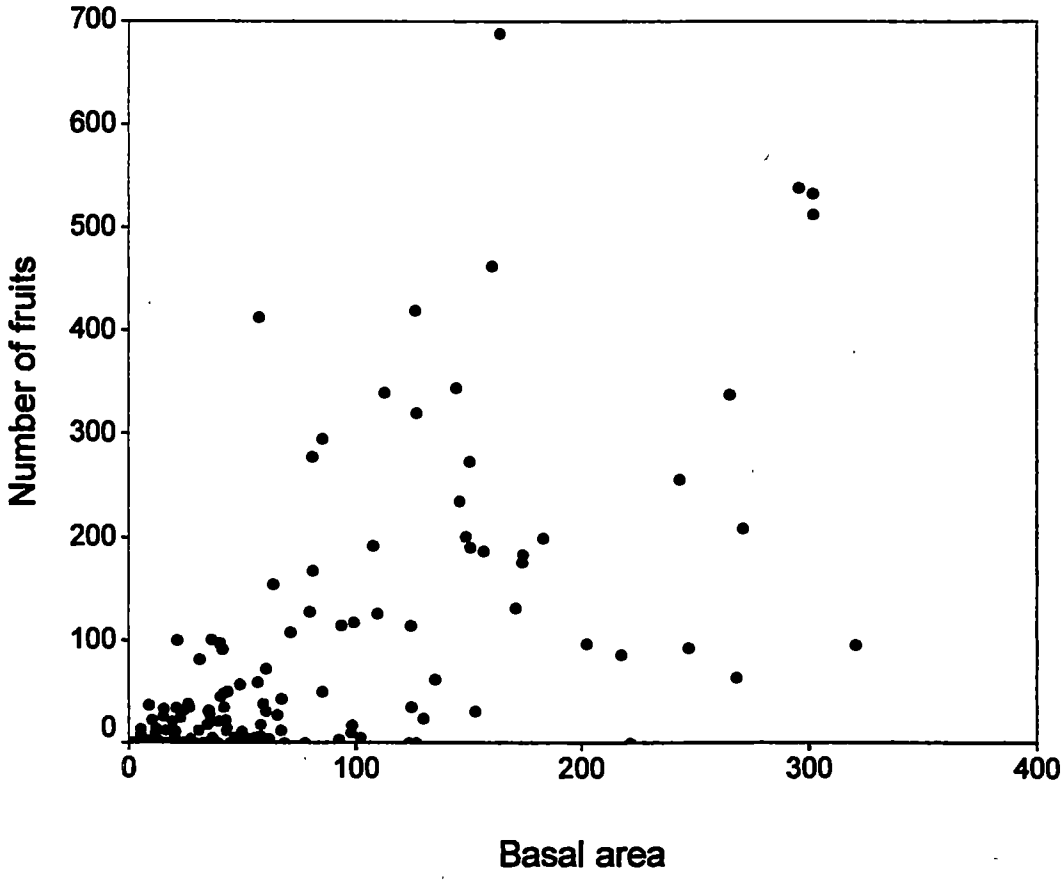


Fig. 2.3 Relationship between number of fruits produced by a plant and its basal area. Data for the Frozen Head site, 1995-1997. $N = 190$; $r = 0.68$; $P < 0.01$.

and largest individuals in a stage differ systematically and substantially in values for demographic parameters such as fecundity and probability of transition to another stage (Moloney 1986; Vandermeer 1978). Stage categories for *A. patula* were established *a posteriori* based on biologically determined form (e.g., seedling), reproductive status, and natural groupings suggested by gaps in the frequency distributions of fecundity, dormancy and mortality by plant size.

Some population matrix projection models include seeds as one of the stages (e.g., Kaliz 1991; Fone 1989; Horvitz and Schemske 1986), which allows the model to incorporate seed dormancy and seed bank dynamics. Laboratory longevity studies of *A. patula* seeds conducted by Carol and Jerry Baskin (University of Kentucky, Lexington, personal communication) on seeds I provided from six populations in east Tennessee indicate the following: 1) a high percentage of seeds produced in the fall season are capable of germinating the following spring, but 2) seeds lose viability after one year.

The present model assumes there is no seed bank and that new seedlings are from seeds produced the previous year. Thus I do not have a seed stage in the demographic model for *A. patula.*

Although dormant vegetative stages have not been explicitly included in published matrix projection models for plants, it seemed prudent to try to account for plant dormancy in the population model developed for *A. patula* for four reasons. First, the frequency of dormancy in some populations was too high to ignore. Second, plant dormancy is potentially important in population dynamics, particularly in relation to stochastic environmental events, such as long periods of drought, heavy grazing pressure, or loss of all stems due to tree branches falling during windstorms. Third, including dormant stages allows many larger but new plants to be included in the population model that otherwise would have to be excluded because they were not

observed previously (i.e., new adult plants appear after the first year of monitoring). Finally, mortality estimates are too high if ability to reemerge is ignored (e.g., an absent plant would have to be considered dead when it is not). A downside to incorporating dormant stages in the model is that I compromised on the guideline of adequate sample size. Valverde & Silvertown (1998) established stages having a minimum of 10 individuals to allow satisfactory estimates of transition probabilities between stages. In the present study, the number of individuals in a given dormant stage was typically less than 10 for most sites and years.

Establishing a reasonable time limit on length of dormancy, and thus designation as dead, is important for matrix population modeling. I considered plants that were absent for more than one year to be dead because >97% of the plants I observed to go dormant reemerged after one year.

Based on the above considerations, nine stages were selected (Table 2.1). Seedlings are in a rosette form. Plants in the stage identified as "nonreproductive" have an elongated stem of small diameter and only rarely produce a few flowers and fruits. The stages A1, A2, and A3 correspond to small, medium and large adult plants that can produce fruits.

Table 2.1 Stages used to describe the population dynamics of *A. patula*. Basal area is the product of number of stems and average stem diameter.

Stage	Abbrev.	Description
Seedling	Sd	Plant form is a rosette; no stem elongation; no flowering
Nonreproductive	NR	Basal area 0.1 - 6.0 mm; typically does not flower
Dormant nonreproductive	NRdor	Plants entering dormancy from the nonreproductive stage
Adult 1	A1	Basal area 6.1 - 15.0 mm; may produce flowers and fruits
Dormant adult 1	A1dor	Plants entering dormancy from the Adult 1 stage
Adult 2	A2	Basal area 15.1 - 56.0 mm; may produce flowers and fruits
Dormant adult 2	A2dor	Plants entering dormancy from the Adult 2 stage
Adult 3	A3	Basal area >56.0-mm; may produce flowers and fruits
Dormant adult 3	A3dor	Plants entering dormancy from the Adult 3 stage

2.5.2 Transition Matrix, Life-cycle Graph, and Transition Probabilities

The general matrix population model is defined by:

$$N(t+1) = A\,N(t)\,,$$

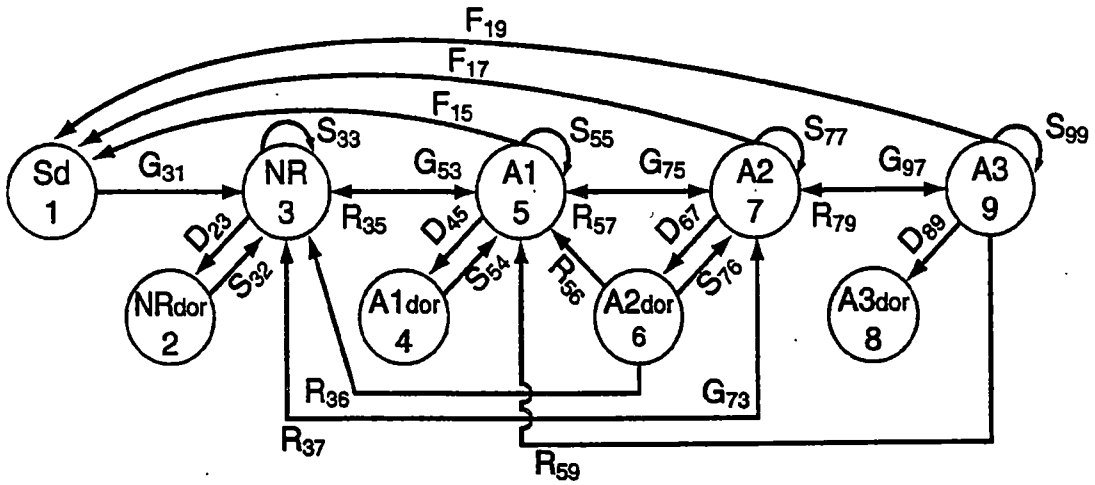
where $N(t)$ and $N(t+1)$ are vectors whose elements are the number of individuals in each of the life stages at time t and $t+1$, respectively, and A is a square matrix whose elements represent transitions from one stage at time t to another stage at time $t+1$.

A life-cycle graph and a corresponding transition matrix (Fig. 2.4) illustrate the impressive variety of potential transitions for the nine stages of *A. patula*. The top row of the transition matrix gives the contribution of the three reproductive stages to the seedling population in year $t + 1$, as well as the probability of a seedling remaining a seedling.

I calculated values for the transition probabilities in this matrix from the field data for each population as the proportion of individuals in stage j (= column j of the transition matrix) at the fall census in year t that were in stage i (row i of the transition matrix) at the fall census in year $t+1$. Because of the inability to accurately census seedlings, the number of seedlings in year t was estimated for each site and year from the number of new nonreproductive plants in year $t+1$ as $Sd(t) = NR(t+1)/G_{31}$, where G_{31} is the probability of growth from a seedling at t to a nonreproductive at $t+1$. I based this estimate on new nonreproductive plants only (i.e., new plants that were nonreproductive) because several transition pathways to the nonreproductive stage occurred other than from the seedling stage (Fig. 2.4). Any new nonreproductive plant is assumed to have come from a seedling that was present, but not necessarily observed, the year before. Although my greenhouse studies indicate that a plant can grow from a seed to the nonreproductive stage within a single growing season under optimal conditions, this transition in the field seems unlikely.

The values for $NR(t+1)$ were based on site- and year-specific counts. However, the same estimate of G_{31} (and of S_{11}, the probability of a seedling remaining a seedling) was

Fig. 2.4 Life-cycle graph for *A. patula* and the corresponding transition matrix (format modified after Valverde and Silvertown 1998, Fig. 1). Circles represent plant stages, arrows represent possible transitions between stages, and labels on the arrows correspond to elements in the transition matrix below. Matrix elements are labeled as follows: F for fecundity (i.e., production of seedlings), G for growth from an above-ground or dormant stage to a larger stage, S for survival in the current stage or reemergence from a dormant stage to an above-ground plant of that same stage, R for regression from an above-ground or dormant stage to a smaller above-ground stage, and D for dormancy from an above-ground stage to a dormant plant of that stage. Matrix elements in bold are included in the life-cycle graph and represent the more common transitions. Matrix elements in italics and underlined are not included in the life-cycle graph; these transitions each account for less than 1% of the total number of transitions. For example, the apparent dead-end transition from A3 to A3dor in the life-cycle graph does not reflect that A3dor plants were observed to reemerge as A2, A1, and nonreproductive plants (elements R_{79}, R_{59} and R_{39} in the transition matrix).



Stage at time *t*

Stage at time *t*+1	Sd	NRdor	NR	A1dor	A1	A2dor	A2	A3dor	A3
Sd	S_{11}	0	0	0	F_{15}	0	F_{17}	0	F_{19}
NRdor	0	0	D_{23}	0	0	0	0	0	0
NR	G_{31}	S_{32}	S_{33}	R_{34}	R_{35}	R_{36}	R_{37}	R_{38}	R_{39}
A1dor	0	0	0	0	D_{45}	0	0	0	0
A1	G_{51}	G_{52}	G_{53}	S_{54}	S_{55}	R_{56}	R_{57}	R_{58}	R_{59}
A2dor	0	0	0	0	0	0	D_{67}	0	0
A2	0	G_{72}	G_{73}	0	G_{75}	S_{76}	S_{77}	R_{78}	R_{79}
A3dor	0	0	0	0	0	0	0	0	D_{89}
A3	0	G_{92}	G_{93}	0	G_{95}	0	G_{97}	S_{98}	S_{99}

used for all 12 site by transition-year matrices. Two data sets, both for Grassy Creek, were available from which to obtain estimates of G_{31} and S_{11}. In a subplot at the east end of the Grassy Creek site, 87 new seedlings were counted and their locations marked with red plastic toothpicks in Fall 1996. In Fall 1997, 32 of these 87 seedlings were still seedlings and 15 were nonreproductives. From these data, $S_{11} = 0.368$ and $G_{31} = 0.172$. In Fall 1997, a total of 189 seedlings (not marked with red toothpicks) were counted for the entire site, including the 32 second-year seedlings. In Fall 1998, 54 new nonreproductives were present.

From this second set of data, a second estimate of $G_{31} = 0.285$. Weighting these two G_{31} estimates by sample size, my best estimate of G_{31} is 0.25. My estimate for S_{11} (to the nearest 0.05) is 0.35. All seedlings in year t that were not seedlings or nonreproductives in year $t+1$ are assumed dead, meaning that the seedling stage experiences a 40% annual probability of mortality (i.e., $1.00 - 0.25 - 0.35$).

The following transitions involving dormant stages were based on a combination of observed data and inferences. Plants other than seedlings are readily observed in the field, although grazing by deer could make smaller plants less conspicuous by the time of the fall census. I felt confident in the census of plants other than seedlings, so any new plant above the nonreproductive stage was assumed to have been dormant in the previous year. Making this assumption allowed me to establish a transition for those individuals and include them in the matrix model.

2.5.3 Reproduction

Estimating the fecundity constants in the first row of each of the 12 transition matrices was a multi-step process (Table 2.2). The non-zero elements (other than S_{11}, the probability of seedling survival) are F_{15}, F_{17}, and F_{19} (Fig. 2.4). Units for these fecundity values are average numbers of seedlings present at a fall census resulting from seeds produced the previous fall by A1, A2, or A3 plants, respectively. The relative fecundity (RF) of each reproductive stage i in year t is calculated as:

$$RF_i(t) = m_i(t) * f_i(t) / \Sigma(m_i(t) * f_i(t)) ,$$

from which $F_{15}(t) = RF_5(t) * Sd(t+1)/A1(t)$, $F_{17}(t) = RF_7(t) * Sd(t+1)/A1(t)$, and $F_{19}(t) = RF_9(t) * Sd(t+1)/A1(t)$. The variable $m_i(t)$ is the fraction of plants in stage A1, A2, and A3 that produced fruit in year t. The variable $f_i(t)$ is an index of the average number of fruits per fruiting plant in stage A1, A2, or A3 in year t. Values for $m_i(t)$ and $f_i(t)$ are estimated from field data for each site-by-year combination (Table 2.2). I have assumed that the number, size and quality of seeds in a fruit are the same for all three reproductive stages. I have no evidence to indicate that the number of seeds or their size or quality change as the size of a parent plant increases. I am assuming that the average number of new seedlings present in a given year, resulting from seeds produced by a reproductive plant the previous year, is directly proportional to the number of fruits produced by that plant. I have ignored the miniscule reproductive contribution of the rare nonreproductive plants that produced a few fruits.

Given how I estimate the number of seedlings by back calculating from the number of new nonreproductives the next year (Sect. 2.5.2), site- and year-specific differences in seed production are implicitly included in the above steps for estimating the three fecundity elements of the 12 site by transition-year matrices. Nonetheless, data on number of seeds per fruit were collected. An analysis of seeds/fruit as a function of site and year is presented in Appendix 3.

2.5.4 Analysis of Matrix Results

RAMAS Metapop software (Akcakaya 1998) was used to calculate the standard demographic characteristics of a population: finite rate of population growth or lambda (λ), stable stage distribution, stage-specific reproductive values, and sensitivity and elasticity matrices (Caswell 1989). It is important to clarify the biological interpretation of λ in demographic analyses involving populations that obviously fluctuate from year-to-year and for which data are available for a limited number of years. Lambda is the

Table 2.2 Calculation of relative fecundity values (RF_i) and fecundity elements (F_{1i}) for the projection matrices for stages A1, A2, and A3 for 1995, 1996, and 1997 for each of the four sites.

Definition of column headings

Col. E is the number of plants listed in Col. D that produced fruit.

Col. F = Col. E/Col. D, i.e., probability of a plant in stage i fruiting.

Col. G is total number of fruit produced by the number of plants listed in Col. E.

Col. H = Col. G/Col. E, i.e., fruits per fruiting plant in stage i.

Col. I = Col. H * Col. F, i.e., the product of the probability of a plant in stage i producing fruit and the number of fruits per fruiting plant in stage i.

Col. J = values in Col. I normalized to sum to 1.0. These values are used to partition the estimated number of seedlings in Col. L among stages A1, A2 and A3.

Col. K is number of new nonreproductive plants observed in year t+2, where year t is specified in Col. B.

Col. L = estimated number of seedlings in year t+1 = 4*Col. K, based on a probability of survival from seedling to nonreproductive of 0.25. See text for estimation of this survival probability.

Col. M = Col. L*Col. J, i.e., number of seedlings produced in year t+1 by plants in stage A_i in year t.

Col. N = Col. M/Col. D, i.e., number of seedlings produced in year t+1 per plant in stage A_i in year t. These $F_{1i}(t)$ values are the fecundity elements in the first row of each site X transition-year matrix.

Other Notes

No plants were observed at the Filtration Pond site in Fall 1997 because of flooding, followed by drought.

In the three rows for 1997 at each site, values for $F_{15}(t)$, $F_{17}(t)$, and $F_{19}(t)$ are calculated as the average of the corresponding F(t) values for 1995 and 1996.

A	B	C	D	E	F	G	H	I	J	K	L	M	N
Site	Year=t	Stage	#Plants(t)	#Fruiting(t)	$m_i(t)$	Totfruit(t)	$f_i(t)$	$m_i(t)*f_i(t)$	$RF_i(t)$	J(t+2)	S(t+1)	$S_i(t+1)$	$F_{ti}(t)$
Clinch River	1995	A1	27	15	0.556	586	39.1	21.7	0.0353	10	40	1.4	0.05
		A2	28	25	0.893	3767	150.7	134.5	0.2185		40	8.7	0.31
		A3	9	9	1.000	4135	459.4	459.4	0.7462		40	29.8	3.32
	1996	A1	20	5	0.250	254	50.8	12.7	0.0206	39	156	3.2	0.16
		A2	29	18	0.621	2119	117.7	73.1	0.1188		156	18.5	0.64
		A3	8	7	0.875	4236	605.1	529.5	0.8606		156	134.3	16.78
	1997	A1	11	4	0.364	216	54.0	19.6	0.0345				0.11
		A2	21	17	0.810	1863	109.6	88.7	0.1558				0.48
		A3	13	12	0.923	5992	499.3	460.9	0.8097				10.05
Filtration Pond	1995	A1	9	6	0.667	84	14.0	9.3	0.0320	0	2	0.1	0.01
		A2	24	23	0.958	1854	80.6	77.3	0.2651		2	0.5	0.02
		A3	19	18	0.947	3892	216.2	204.8	0.7029		2	1.4	0.07
	1996	A1	3	0	0.000	0	0.0	0.0	0.0000	27	108	0.0	0.00
		A2	26	17	0.654	512	30.1	19.7	0.1822		108	19.7	0.76
		A3	25	20	0.800	2209	110.5	88.4	0.8176		108	88.3	3.53
	1997	A1											0.00
		A2		No vegetative plants observed because of flooding, followed by a drought									0.39
		A3											1.80
Frozen Head	1995	A1	7	3	0.429	41	13.7	5.9	0.0245	1	4	0.1	0.01
		A2	18	12	0.667	487	40.6	27.1	0.1131		4	0.5	0.03
		A3	24	21	0.875	4952	235.8	206.3	0.8624		4	3.4	0.14
	1996	A1	10	0	0.000	0	0.0	0.0	0.0000	5	20	0.0	0.00
		A2	21	12	0.571	306	25.5	14.6	0.0819		20	1.6	0.08
		A3	20	18	0.900	3268	181.6	163.4	0.9181		20	18.4	0.92
	1997	A1	16	7	0.438	55	7.9	3.4	0.0200				0.01
		A2	22	16	0.727	452	26.3	20.5	0.1195				0.05
		A3	20	20	1.000	2958	147.9	147.9	0.8605				0.53
Grassy Creek	1995	A1	27	8	0.296	187	23.4	6.9	0.0190	67	268	5.1	0.19
		A2	17	9	0.529	884	98.2	52.0	0.1425		268	38.2	2.25
		A3	1	1	1.000	306	306.0	306.0	0.8385		268	224.7	224.73
	1996	A1	22	12	0.545	301	25.1	13.7	0.0558	28	112	6.2	0.28
		A2	22	19	0.864	782	41.2	35.5	0.1449		112	16.2	0.74
		A3	2	2	1.000	392	196.0	196.0	0.7993		112	89.5	44.76
	1997	A1	14	6	0.429	60	10.0	4.3	0.0374				0.24
		A2	30	18	0.600	1246	69.2	41.5	0.3620				1.49
		A3	10	6	0.600	689	114.8	68.9	0.6006				134.74

asymptotic growth rate associated with a given matrix of transition probabilities. Interpreting lambda as a prediction of future growth, however, would be valid and perhaps useful only if the environment and all demographic characteristics remained constant, which we know is not the case. It is conceptually more sound to consider lambda a synthesis of all the demographic characteristics observed during a given transition interval into a single parameter, an overall measure of demographic success (Horvitz and Schemske 1995).

The effect on λ of each a_{ij} in the transition matrix is evaluated through a combination of sensitivity and elasticity analyses. Sensitivity analyses help identify crucial demographic processes influencing population growth rate. The effect on λ of small changes in the elements of the transition matrix is given by the sensitivity matrix (Caswell 1989). The elasticity matrix is a sensitivity matrix whose elements have been standardized to allow comparison of matrix elements having different numerical scales. Although both fecundities and transition probabilities have a lower bound of zero, transition probabilities have an upper bound of 1.0, whereas fecundities may be considerably greater than 1.0. The sum of all the values in the elasticity matrix equals unity, which provides a useful basis for comparing the relative contribution of different stage-specific, life-cycle processes (e.g., fecundity, growth, survival, regression, and dormancy) to population growth rate.

Log-linear analysis was used to test the null hypothesis that the distribution of plants among stages is independent of site and year, versus the alternative hypothesis that the stage distributions differ significantly as a function of site, year, or their interaction. Standard log-linear analysis techniques for hierarchical models were used (SPSS Inc. 1997; Caswell 1989; Fingleton 1984). Separate analyses were performed for observed stage distributions in different years, stable stage distributions for different transition periods, and observed distributions in year $t+1$ versus stable distributions for transition period t to $t+1$.

The stable stage distribution gives the proportion of the projected population in the various stages. The transition probabilities determine the stable stage distribution, regardless of initial stage frequencies. To examine the degree of similarity between observed and stable stage distributions, I calculated the proportional similarity index (*PSI*) for each of the 12 site by transition-year combinations (Horvitz & Schemske 1995).

$$PSI = \Sigma min(O_i - S_i) * 100,$$

where the summation is over all stages i (except seedlings) of the minimum of O_i and S_i, O_i is the proportion of plants in stage i of the observed stage distribution, and S_i is the proportion of plants in stage i of the stable stage distribution. The seedling stage was not included because the abundance of seedlings is calculated rather than observed (Sect. 2.5.2)

2.6 Population Model Results

The results of the analysis of population projection matrices are given in Appendix 4. Population growth rate (λ), stable stage distribution, reproductive values, and sensitivity and elasticity matrices are reported for each site by transition-year combination. Three transition years were used to characterize population dynamics and structure: 95-96, 96-97, and 97-98. The transitions for the FP population for years 96-97 and 97-98 were influenced by an unusual flood event and show high mortality and transition to dormancy by the surviving individuals (96-97) and transition from dormancy (97-98). Thus these transition years at FP represent atypical dynamics under normal environmental circumstances and present an opportunity to evaluate the response of *A. patula* to an environmental catastrophe.

2.6.1 Population Growth Rate

Population growth rates (λ) vary by population and year (Fig. 2.5). For eight of the 12 site by transition-year combinations, the values are at or above 1.0, indicating

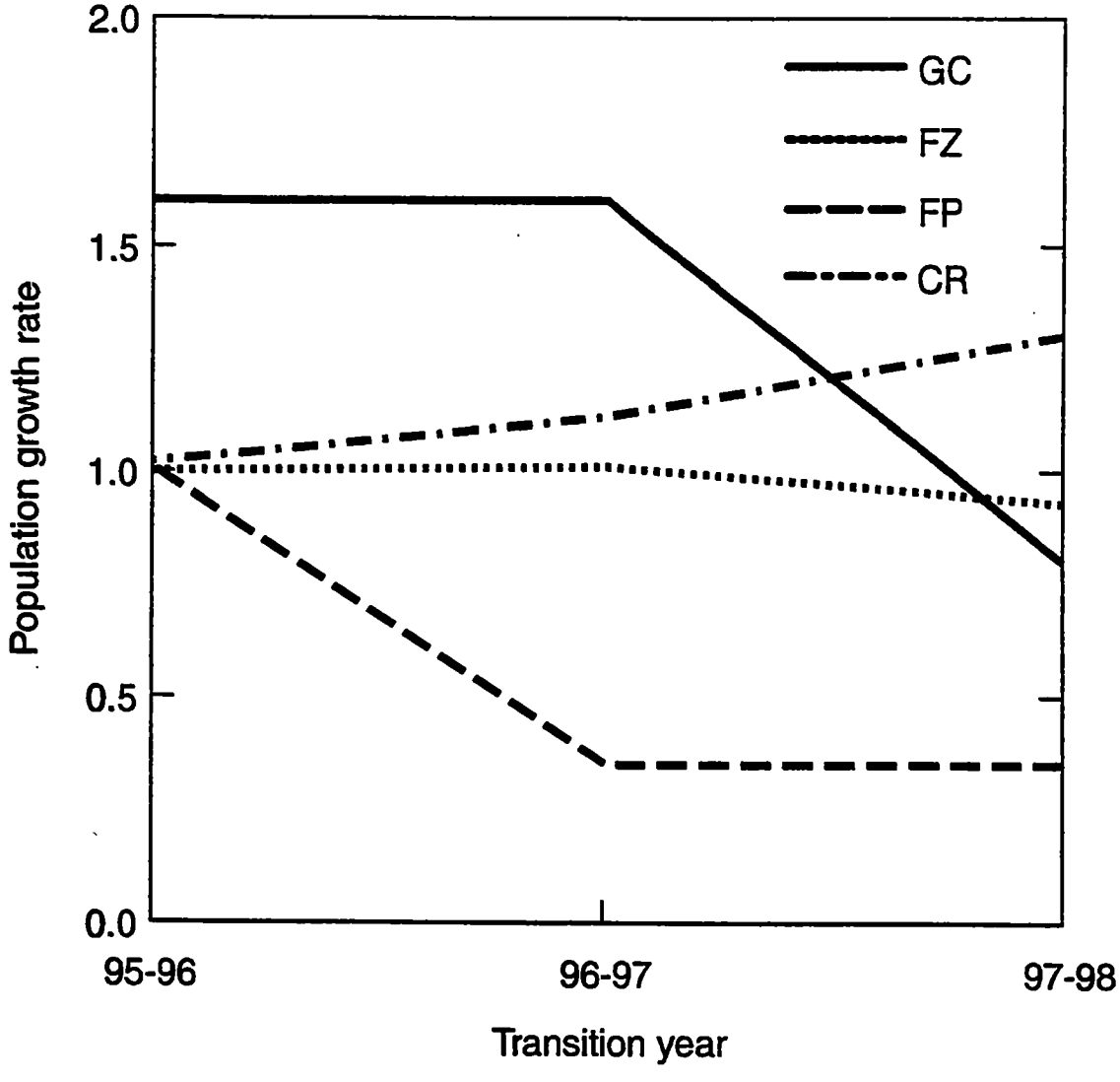


Fig. 2.5. Population growth rate for each transition year and site, as measured by λ. The *A. patula* populations at the four sites (CR, FP, FZ and GC) are represented by separate lines.

population stability or growth for those transition years. The low values for FP (0.35) for two transition years reflect high mortality and transition to and from dormant stages in response to a long duration flood and drought during 96-97. The highest values of λ (~1.60 for GC for two years) reflect the large number of seedlings advancing to the nonreproductive stage. A reduced number of growth transitions contributed to the decline in λ for GC in transition-year 97-98.

2.6.2 Observed- and Stable-stage Distributions

Results of the log-linear analyses for both the 16 observed stage distributions and the 12 projected stable stage distributions indicate that the distribution of plants among the nine stages is significantly influenced by site, year, and the interaction of these two explanatory factors (Table 2.3). The 16 observed distributions are shown in Fig. 2.6. Note that observed seedling bars are absent in the last column (1998 column) of Fig. 2.6. Number of seedlings was not calculated for 1998 because my field study did not continue into 1999 to include counts of new nonreproductive plants from which to estimate number of seedlings in 1998. The statistically significant effect of site on observed distributions can be visualized by comparing the black bars in the four rows. For example, larger plants were relatively common at FZ and relatively rare at GC. The significant effect of year on observed distributions can be visualized by comparing the black bars in the three columns. For example, the pattern of stage distributions at CR, FP, and GC is quite different in each of the three years; FZ is the only site with a similar pattern of stage distribution across years. At FP in 1997, the observed distribution indicates that all plants except late emerging seedlings were in dormant stages.

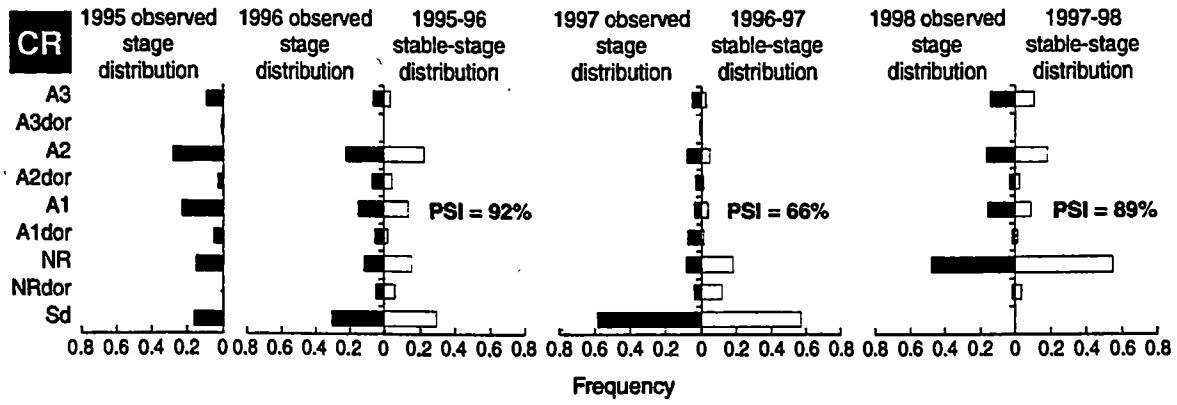
An analogous visual comparison of the stable stage distributions illustrates the basis for their differing significantly by site and by year. For example, the stable stage distribution at FZ is relatively uniform across stages for all three years, while the stable stage distribution at GC is more dominated by smaller plants for all three years. The significant effect of the site-by-year interaction on the observed and stable distributions indicates that in addition to the main effects of site and year, the pattern of how plants

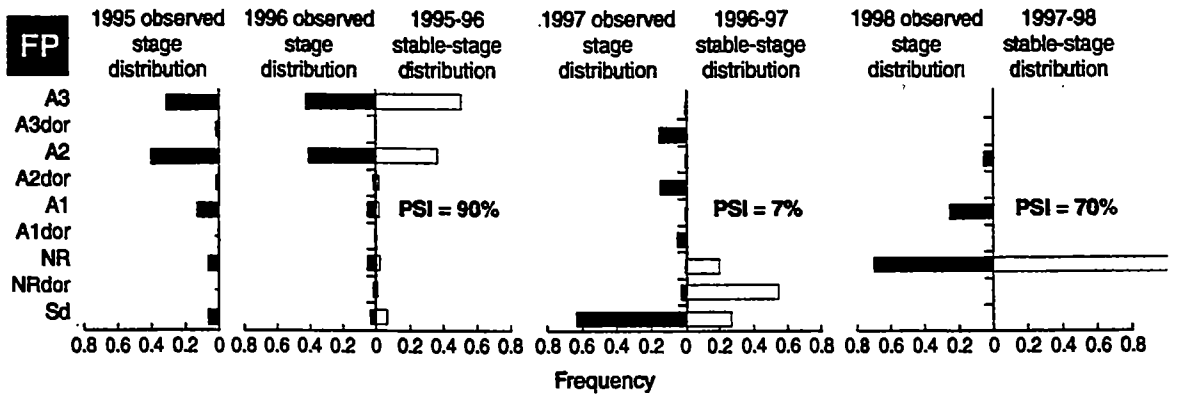
Table 2.3 Results of log-linear analyses for alternative models of observed stage distribution (number of plants observed in each stage category of *A. patula*) at four sites for four years, and of stable stage distribution projected by the population model at four sites for three transition years. The explanatory variables are 'site' (CR, FP, FZ and GC) and 'year' (1995, 1996, 1997 and 1998) or transition year (1995-96, 1996-97, and 1997-98). The response variable is 'stage' (NRdor, NR, A1dor, A1, A2dor, A2, A3dor, and A3). The seedling stage is not included because the number of seedlings is estimated rather than observed. The statistical significance of each explanatory variable is analyzed by examining the reduction in G^2 (i.e., ΔG^2) when each explanatory variable is added to a model that excludes it.

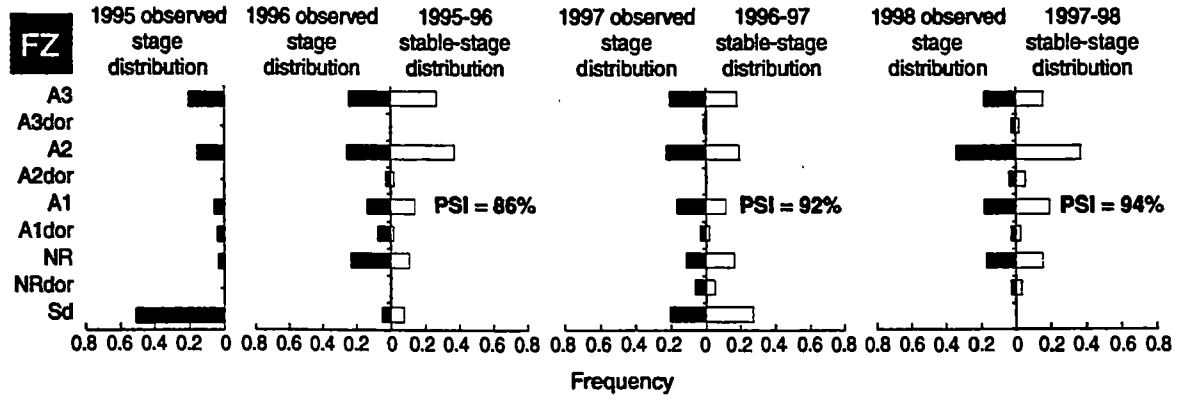
	Observed stage distributions			Stable stage distributions		
Model	**df**	**G^2**	**P**	**df**	**G^2**	**P**
site X year, site X stage, year X stage	63	387		42	2509	
site X year X stage	0	0.0		0	0.0	
site X year X stage	63	387	0.000[a]	42	2509	0.000[a]
site X year, year X stage	84	684		63	5375	
site X year, site X stage, year X stage	63	387		42	2509	
site X stage	21	297	0.000[b]	21	2866	0.000[b]
site X year, stage	105	940		77	8292	
site X year, site X stage	84	643		56	5412	
site X stage	21	297	0.000[b]	21	2880	0.000[b]
site X year, site X stage	84	643		56	5412	
site X year, site X stage, year X stage	63	387		42	2509	
year X stage	21	256	0.000[c]	14	2903	0.000[c]
site X year, stage	105	940		77	8292	
site X year, year X stage	84	684		63	5375	
year X stage	21	256	0.000[c]	14	2917	0.000[c]

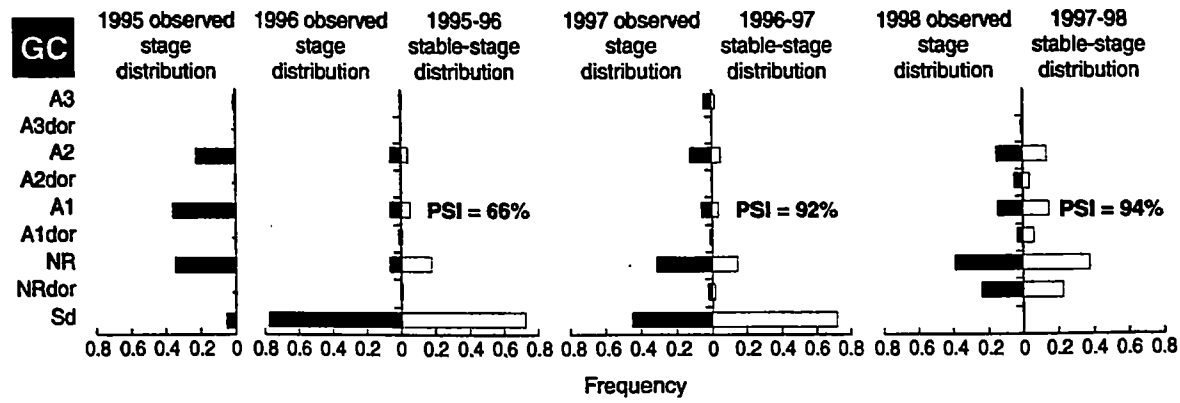
[a] Probability the interaction effect of site and year on stage distribution is zero.
[b] Probability the conditional and marginal effects of site on stage distribution is zero.
[c] Probability the conditional and marginal effects of year on stage distribution is zero.

Fig. 2.6 Comparison of observed and stable stage distributions for the three transition years at each of the four sites. The stable distribution for each transition year is compared to the observed distribution at the end of that transition year. The observed stage distribution for 1995 has been included to facilitate visual comparison of the four observed distributions at each site. The seedling stage is not included for 1997-98. Frequencies are relative, i.e., the sum of the bars for each distribution equals 1.0. PSI is the proportional similarity index between stable and observed distributions, calculated without including the seedling stage.


CR
1995 observed stage distribution
1996 observed stage distribution
1995-96 stable-stage distribution
1997 observed stage distribution
1996-97 stable-stage distribution
1998 observed stage distribution
1997-98 stable-stage distribution
A3
A3dor
A2
A2dor
A1
A1dor
NR
NRdor
Sd
PSI = 92%
PSI = 66%
PSI = 89%
0.8 0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
Frequency


FP
1995 observed stage distribution
1996 observed stage distribution
1995-96 stable-stage distribution
1997 observed stage distribution
1996-97 stable-stage distribution
1998 observed stage distribution
1997-98 stable-stage distribution
A3
A3dor
A2
A2dor
A1
A1dor
NR
NRdor
Sd
PSI = 90%
PSI = 7%
PSI = 70%
0.8 0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
Frequency


FZ
1995 observed stage distribution
1996 observed stage distribution
1995-96 stable-stage distribution
1997 observed stage distribution
1996-97 stable-stage distribution
1998 observed stage distribution
1997-98 stable-stage distribution
A3
A3dor
A2
A2dor
A1
A1dor
NR
NRdor
Sd
PSI = 86%
PSI = 92%
PSI = 94%
0.8 0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
Frequency


GC
1995 observed stage distribution
1996 observed stage distribution
1995-96 stable-stage distribution
1997 observed stage distribution
1996-97 stable-stage distribution
1998 observed stage distribution
1997-98 stable-stage distribution
A3
A3dor
A2
A2dor
A1
A1dor
NR
NRdor
Sd
PSI = 66%
PSI = 92%
PSI = 94%
0.8 0.6 0.4 0.2 0 0.2 0.4 0.6 0.8
Frequency

are distributed among the stages is affected by the particular combinations of site and year.

Comparison of the stable and observed stage distributions provides insight into the applicability of population model output (λ, reproductive values, etc.) to the single transition-year observed dynamics. If observed and stable stage distributions are similar, then model output more closely portrays the dynamics of the observed population. Comparison of observed and stable stage distributions for each site and transition-year combination indicates an impressive degree of similarity in most cases (Fig. 2-6). The proportional similarity index (PSI) exceeds 80% for eight of the 12 comparisons, and exceeds 90% for five of these comparisons (mean PSI = 86.3 %, SE = 3.5%, N = 10, excluding the two years influenced by flooding at FP). The high average similarity between projected stable and observed stage distributions means that the other output of the matrix projection model (λ, reproductive value, and sensitivity and elasticity matrices) represents most of the one-year dynamics of the four populations to a reasonable extent

2.6.3 Reproductive Values

Reproductive values (RV), which indicate the contribution of each stage in producing offspring in current and future years, vary by site and transition-year (Fig. 2.7 and Appendix 4). Across all sites and transition-years, RV increases as plant size increases, which reflects increasing fecundity and decreasing probability of mortality in the larger size classes. The A3 stage has the highest RV at all sites. The highest value (~175) is at Grassy Creek in transition-year 97-98. Relatively high fruit production by A3 plants occurred in 1997 at GC. No value for RV of stage A3 at GC in 95-96 is presented because small sample size and lack of mortality in that stage led to infinite residence time in the model for the A3 stage, a biologically unrealistic case. It is clear that population-level fecundity at GC is dominated by larger plants, especially the A3 stage.

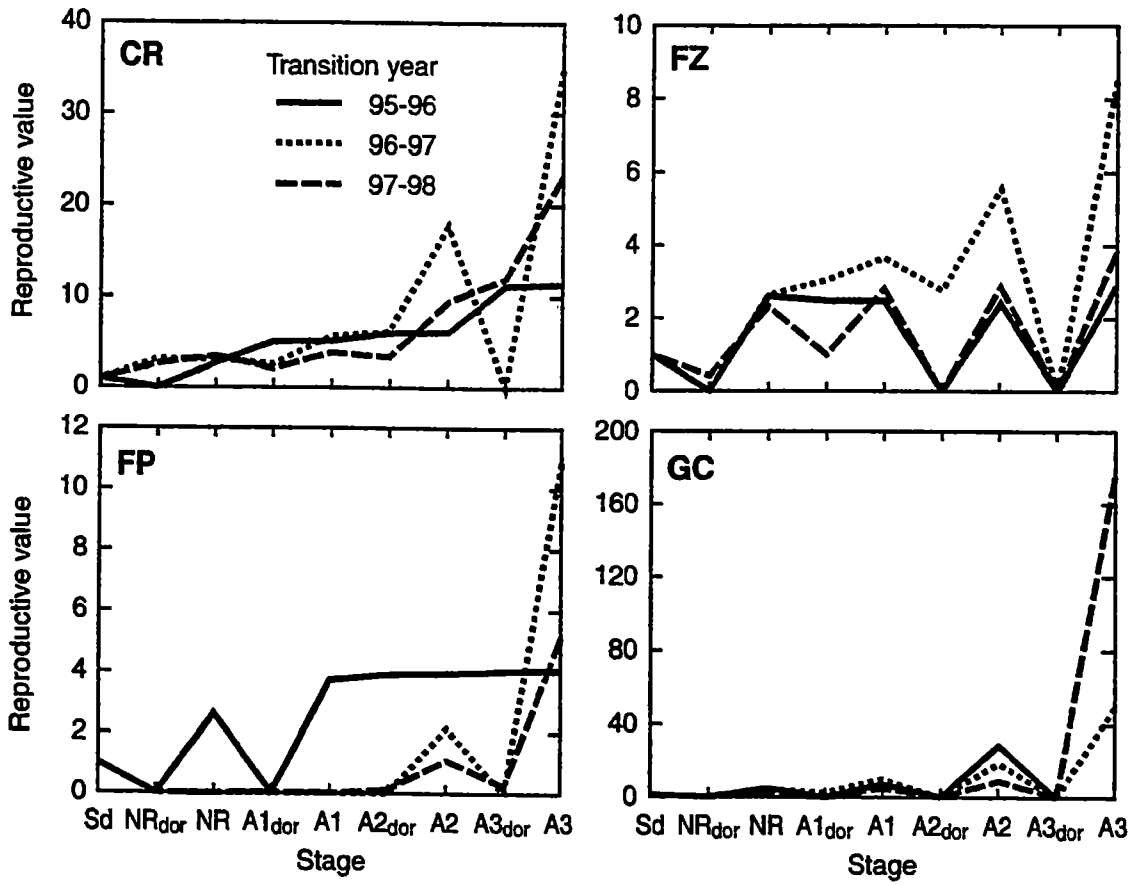


Fig. 2.7 Stage-specific reproductive values for *A. patula* populations at the four sites for each of the three transition years. The values for each stage are scaled relative to the reproductive value of a seedling, the value of which is 1.0. CR = Clinch River site; FP = Filtration Pond site; FZ = Frozen Head site; GC = Grassy Creek site.

The RV's of the dormant stages reflect the frequency of their occurrence and the probability of reemergence at the various sites. During the duration of my demographic study, there were no cases of reemergence from dormancy at GC, consequently all the dormant stages have a RV of zero. At FZ in all transition-years the RV of stage A3dor is zero, while at CR and FP that stage shows nonzero values in two of the three transition years. The frequency of occurrence of A3dor at FZ is very low, and there are no cases of reemergence from A3dor at FZ. At CR and FP occurrence of dormancy and reemergence from the A3dor stage are more common. A1dor and A2dor had nonzero values in some transition years, with the highest values occurring at CR, where dormancy is a more common transition. RV for NRdor is low for all sites and transition-years, which is consistent with poor reemergence from that stage.

2.6.4 Sensitivities and Elasticities

Sensitivity and elasticity matrices for each of the 12 site by transition-year combinations are given in Appendix 4. The highest sensitivities are most commonly associated with the two larger adult classes (A2 and A3). High sensitivities for transitions from A2 to A3 and survival of A3 make biological sense in that these two stages typically have relatively low mortality and are the major producers of seed. The large sensitivities for the transitions from seedlings, dormant nonreproductives, and nonreproductives to A3 do not make biological sense in that they represent impossible transitions and appear as structural zeros in Fig. 2.4. Sensitivities varied among the four sites. For example, for all three transition years the highest sensitivities were < 1.0 at the FZ site, but > 10.0 at the GC site.

I found the elasticities to be considerably more useful in analyzing the dynamics of these *A. patula* populations. I summed the elasticities from selected regions of each elasticity matrix in order to collapse the numerous individual values into categories representing important processes in the life cycle of this species. The categories are fecundity, growth, survival, regression, and dormancy (Table 2.4 and Fig. 2.4).

Table 2.4 Summary of results from the elasticity matrices for the 12 site X transition-year combinations (see Appendix 4 for the individual matrices). Elasticities have been summed from selected regions of each elasticity matrix. Using Fig. 2.4 as a guide, Fecundity is a summation of the three F_{1j} elasticities in the first row; Growth is a summation of G_{ij} elasticities below the diagonal; Survival is a summation of S_{ij} elasticities along and adjacent to the diagonal; Regression is a summation of R_{ij} elasticities above the diagonal; and Dormancy is a summation of the four D_{ij} elasticities adjacent to the diagonal. The column headed Survival+ is a summation of the survival, regression and dormancy elasticities.

Site-Year	Fecundity	Growth	Survival	Regression	Dormancy	Survival+
CR 95-96	0.054	0.294	0.413	0.129	0.109	0.652
CR 96-97	0.113	0.404	0.306	0.047	0.131	0.484
CR 97-98	0.114	0.374	0.442	0.043	0.027	0.512
FP 95-96	0.011	0.146	0.701	0.127	0.015	0.843
FP 96-97	0.000	0.000	1.000	0.000	0.000	1.000
FP 97-98	0.000	0.000	1.000	0.000	0.000	1.000
FZ 95-96	0.021	0.261	0.479	0.219	0.021	0.719
FZ 96-97	0.047	0.271	0.560	0.105	0.017	0.682
FZ 97-98	0.040	0.295	0.514	0.137	0.014	0.665
GC 95-96	0.129	0.437	0.416	0.018	0.000	0.434
GC 96-97	0.152	0.546	0.258	0.042	0.002	0.302
GC 97-98	0.095	0.326	0.514	0.065	0.000	0.579

Dormancy was most common at the CR site, and this is reflected in the dormancy elasticities being greatest for that site. This result means that λ is relatively sensitive to changes in dormancy at the CR site, whereas dormancy is less important at the other sites, particularly at the GC site, where dormancy rarely occurred (Table 2.4). Regression elasticities were highest in transition year 95-96 at CR and FZ, but lowest at GC in that year. Thus regional environmental conditions are not a plausible explanation for population level regression, unless the regional conditions affected sites differently. The elasticities for fecundity and growth are highest in transition years 96-97 and 97-98; elasticities for both of these demographic processes are relatively high at CR and GC sites, compared to the FP and FZ sites. Population growth rate was more sensitive to survival transitions at FP and FZ relative to CR and GC.

2.7 Discussion

Population growth rates varied among sites and years, making summary projections of future growth rate questionable, even for a given site. Although observed and stable stage distributions were similar within a site for each of the three transition-years, the among site and among transition-year variabilities were significant. Biotic and abiotic factors at each site and environmental variability from year to year affected stage distributions, thus precluding a general definition of expected stage distributions in *A. patula* populations. The stages having the greatest influence on λ also varied by site and transition-year. However, evaluation of these crucial stages using the elasticity matrices provides insights into population trends.

Population vital rates, as determined by λ values for the 12 site by transition-year combinations, are constant neither among sites nor across years at a site (Fig. 2.5). At two sites, the projected growth rate indicates stability or growth for consecutive years (GC and FZ for transition-years 95-96 and 96-97), but λ for the following transition-year (97-98) indicates population decline. The CR site showed growth across all three transition-years. The catastrophic flood at the FP site resulted in a dramatically lower population growth rate in the year of the flood (1997) and the following year. All these

examples indicate that the λ value for a given transition-year is a poor predictor of population behavior in the following year or further into the future.

Elasticity matrices indicate that at some sites (FZ and FP) survival of the larger adult stages has the greatest influence on λ. For the CR site, changes in survival of larger adult stages and survival from nonreproductive to nonreproductive, combined with growth from A2 to A3 stages, had the greatest influence on λ. At the GC site, growth from A2 to A3 and from Sd to NR, along with survival of the A3 stage and fecundity of the A3 stage, were important contributors to the population growth rate during 95-96 and 96-97. In transition-year 97-98 at GC, survival of the A2 stage and growth from A1 to A2 and from NR to A1 had the greatest influence on λ. In summary, it appears that the projected growth rate of populations at some sites (FP and FZ) is heavily influenced by survival and growth of larger stages, while at other sites population growth rate is influenced by survival and growth of a range of stages (CR and GC).

The elasticity analyses showed a high degree of dependence of λ on fecundity only for the GC site and only for the fecundity of stage A3. At the CR site, the elasticity value for fecundity was not one of the highest but was not as low as the values for FP and FZ. As for the GS site, the fecundity of stage A3 was the most important of the fecundity effects on λ.

The elasticity analyses indicate that the most critical life stages vary across space and time. Other investigators have reported similar results (Menges and Dolan 1998; Valverde and Silvertown 1998; Kephart and Paladino 1997; Horvitz and Schemske 1995; Bierzychudek 1982). The most critical life stage for rare species is sometimes viewed as distinct and unvarying, e.g., inability of reproductive stages of a non-clonal species to produce sufficient seed. Identifying the most critical life stage and determining the causes for variation in that stage has been seen as a goal for conservation-based demographic studies (Schemske et al. 1994). For species such as

A. patula that exhibit great spatiotemporal variability in demographic characteristics, investigating the factors that influence this variability is a research priority.

In some cases habitat differences can explain much of the variability in critical life stages within years. These differences have been attributed to management regime such as periodic burning (Menges and Dolan 1998). In burned sites growth elements of the transition matrix dominated the elasticity matrices of *Silene regia*, whereas at unburned sites, survival elements were most important. In other cases amount of diffuse light explained variability in the life stages with the most influence on population growth rate. Greater light was associated with higher elasticities for growth elements in the understory herb, *Primula vulgaris*, while survival elements were more important in darker patches (Valverde and Silvertown 1998).

Although my study was not designed to investigate the effects of specific environmental factors in accounting for variability in the population dynamics of *A. patula*, my results suggest that light alone seems a poor predictor of population growth for *A. patula* among sites. The sites showing the greatest contribution of growth and fecundity to λ were the most moist, shaded site (GC) and the most open, dry site (CR). However, these sites share the characteristic of being moderately steep (slopes from 15 to 16%). Lack of deep litter and access to mineral soil exposed during slope erosion may be crucial to seedling establishment.

Ecologists seek to observe pattern in the biotic and abiotic world and identify processes that influence that pattern. In some cases pattern is detected through analysis rather than direct observation. Silvertown et al. (1992) introduced a new approach to characterizing the variety of life histories found among plants by proposing a demographic classification of species (and populations within species; see Valverde and Silvertown 1998) based on three composite elasticities. Silvertown et al. (1992, p. 130) comment that "the virtue of a demographic approach to life-history strategies is that demographic variables can be used to calculate the fitness of a life-history phenotype.

Three demographic processes contribute to the finite rate of increase (λ) of a population: fecundity (F), growth (G) and survival (L) [L = S+ in my symbolism]." Other researchers have since found this framework to be a useful approach for evaluating the relative importance of these life-cycle components, while reducing potentially confounding effects associated with the particular stage categorization selected (Menges and Dolan 1998; Valverde and Silvertown 1998; Enright et al. 1995).

I summed my survival, regression, and dormancy elasticities to give a composite survival elasticity (S+) that is approximately equivalent to that of Silvertown et al. (1992). It seemed biologically reasonable to include both regression and dormancy as a form of survival. Disregarding the data for the FP site in transition years 96-97 and 97-98, I plotted the other 10 triplets of (F, G, S+) values in Table 2.4 using the demographic triangle (Silvertown et al.1992) (Fig. 2.8). The points all lie in a narrow band of fecundity values (0.01 to 0.15) along the right side of the triangle. Because the sum of these three composite elasticities must sum to 1.0, the remaining 0.85 to 0.99 elasticity is split between growth and survival. The growth elasticities are less than survival elasticities, except for the GC site in 96-97. Differences among the four sites appear to be more pronounced than differences among the three transition years. In particular, growth/survival elasticities are variable for GC and CR, while for FZ they are closely clustered. The dynamics of the population at GC and CR are more varied over time than the population at FZ, which is based primarily on survival of the larger size classes. The single plotted value for FP indicates an even higher importance of survival transitions relative to fecundity and growth.

Silvertown and colleagues (1992, 1993) investigated pattern in demographic and life-history traits for various groups of perennial plants: semelparous herbs, iteoparous herbs of open habitat, iteoparous forest herbs, and woody plants. By plotting values of the composite elasticities for F, G, and S+ on the demographic triangle (see Fig. 2.8), they have identified spatial regions within the graph occupied by different groups. Semelparous herbs, which have a single episode of flowering during their lifetime, have high fecundity and growth elasticities and occupy the upper left region of the graph.

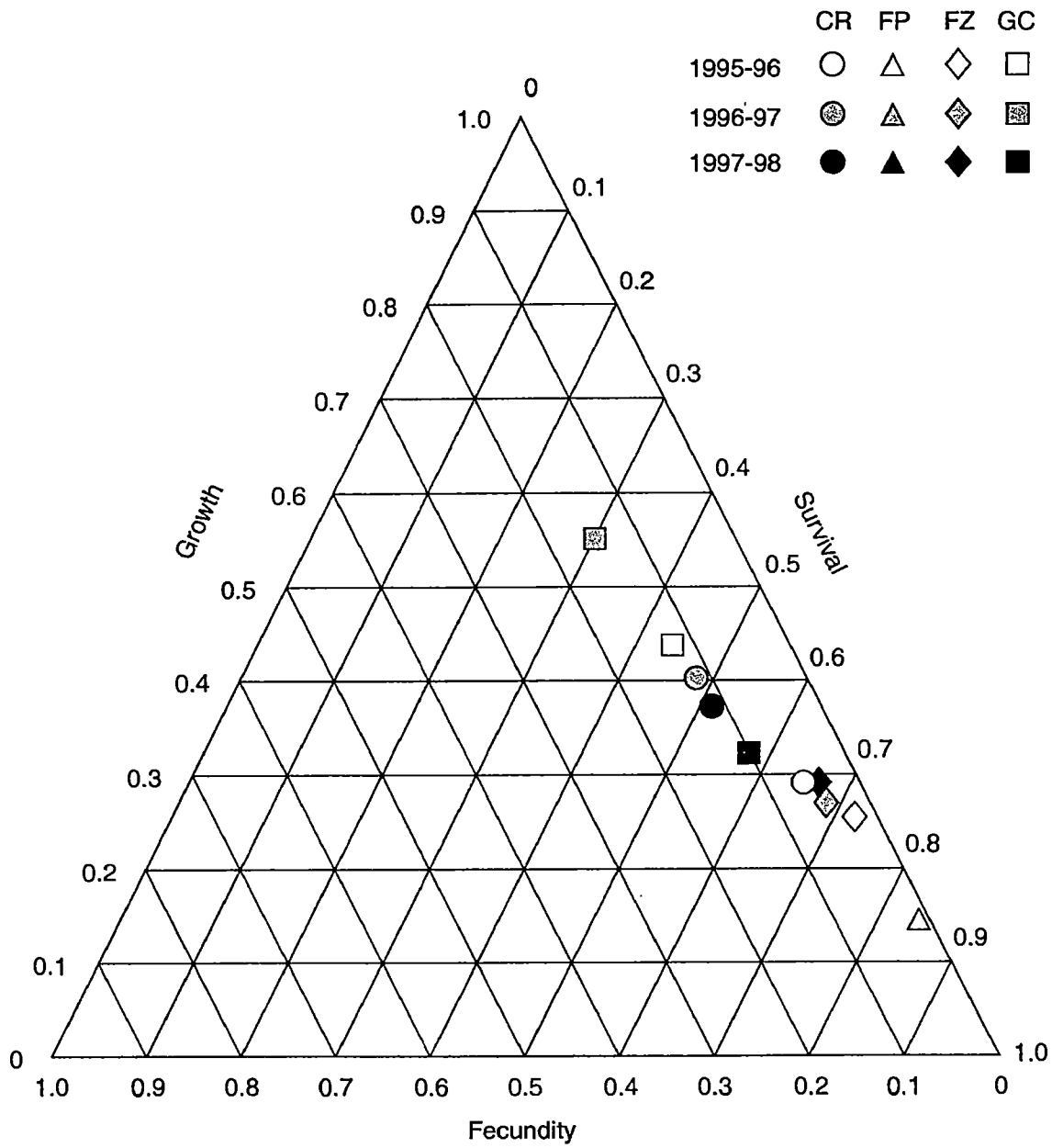


Fig. 2.8. Triangular graph of fecundity, growth and survival elasticities for the four sites and three transition years. Data for the FP site in 1996-97 and 1997-98 have not been plotted (see Table 2.4). The points are coded as follows: For site, circle = CR; triangle = FP; diamond = FZ; and square = GC. For transition year, open = 1995-96; gray = 1996-97; and black = 1997-98.

Semelparous herbs include species in the genus *Agave* that grow for years, flower, and then die. Iteoparous herbs are those with multiple reproductive efforts in their lifetime, typical of many perennials. Iteoparous herbs of open habitat occur in the middle regions of the graph, reflecting moderate values for all parameters. Iteoparous forest herbs have low values for fecundity elasticities and variable values for growth and survival; their plotted region is to the far right side of the triangular space and extends in a linear fashion, similar to that shown in Fig. 2.8. Woody plants, particularly trees, tend to cluster in the region defined by very low fecundity elasticities and very high survival elasticities, toward the bottom right-hand corner of the graph. Overall, *A. patula* fits the pattern found for iteoparous forest herbs.

In the present study it may be most useful to look at demographic trends of the various site by transition-year samples in the context of F, G, and S+ space. The population at GC in year 96-97 shows trends more similar to iteoparous herbs of open habitats; in 95-96 and 97-98 at GC the demographic traits fit those identified for iteoparous forest herbs. For all three transition-years, the plotted values for CR lie within the region occupied by iteoparous forest herbs. The three plotted values for FZ and the single value for FP is closer to the region associated with woody plants than to iteoparous forest herbs. Clearly populations of *A. patula* vary somewhat over time and space in their apparent demographic strategy, as has been reported for other species (Menges and Dolan 1998; Valverde and Silvertown 1998; Horvitz and Schemske 1995).

Although recognition of separate spatial regions in the F,G, and S+ demographic triangle for different functional groups may help develop rules of thumb for conservation efforts, especially when species specific data are not available, elasticity analyses must be interpreted carefully when used to prescribe conservation actions (Silvertown et al. 1996). For example, a demographic study of populations of a rare iteoparous herb threatened with habitat alteration might reveal low fecundity and growth elasticities and high survival elasticities. The best actions might appear to be those that enhance survival of existing individuals. However, without recruitment of

new individuals in some years, the populations will eventually be lost. Thus working only to enhance survival will not result in successful persistence of the species. Evaluating the λ values associated with particular elasticity values helps in the interpretation of needed action. For example, population growth rates at or less than 1.0 for populations with high survival elasticities and low fecundity and growth elasticities suggest that conservation actions must enhance the fecundity and growth transitions.

In summary, this study indicates that most of the four populations for most years were increasing in size, but projected population growth rates are variable and not all above 1.0. For most site-by-transition-year combinations the observed and stable stage distributions were similar, although both observed and stable distributions varied significantly by site, year, and site-by-year interaction. The data analyses indicate that populations are variable in the relative importance of the key demographic processes of fecundity, growth, and survival. Too much variability was observed to make overall projections about population dynamics or persistence. Demographic patterns would likely be more evident if these four populations were followed for a decade or more, but the generality of these patterns would need to be evaluated by monitoring additional populations at similar and different types of sites.

One of the most important results of this demographic study is information gained about the life history of *A. patula*. Individuals demonstrate considerable plasticity in possible transitions, including rapid growth (transition from nonreproductive to A3), dramatic regression (transition from A3 to nonreproductive), and dormancy. Dormancy was particularly important at two sites, CR and FP. At CR dormancy was a relatively common occurrence on an annual basis and an important influence on projected population growth rate in some years. At FP, dormancy was observed primarily in response to an episodic event. Although the flood at the FP site was frustrating to me because it rendered two years of demographic data from that site unusable in many comparisons, it was a good example of population-level response of *A. patula* to site-specific environmental catastrophe. The ability to withstand stressful conditions by

becoming dormant appears to have high survival value; most of the plants not killed by the flood did reemerge from dormancy in 1998, although many regressed in size. At all sites and across years, regression was not an uncommon transition, even without dormancy as a prelude. The large number of possible transitions between stages indicates *A. patula* is able to respond to favorable conditions rapidly and survive unfavorable conditions by becoming a smaller above-ground plant or by going dormant.

Chapter 3. Host – Hemiparasite Interactions of *Aureolaria patula* and *Aureolaria virginica.*

3.1 Introduction

Parasitic plants as a group represent a fascinating evolutionary shift in life history strategy, a reversal from an autotrophic to a primarily heterotrophic mode of nutrition. There are approximately 3000 species of parasitic angiosperms in 15 families worldwide (Press et al. 1990; Watkinson and Gibson 1988), and for convenience in discussion they are usually classified into two groups, holoparasites and hemiparasites. Holoparasites have little to no chlorophyll and apparently depend solely on a host for acquisition of water, minerals and organic compounds necessary for growth and reproduction. Hemiparasites contain chlorophyll and are capable of solely autotrophic living for at least some portion of their life histories, typically from the time of germination until the seedling connects to a host. Connection is by means of specialized structures called haustoria that allow the parasite to access the vascular system of the host (Kuijt 1969).

Stem hemiparasites, commonly called mistletoes, attach to the stems of their hosts; thus their parasitic nature is usually evident. Root hemiparasites, on the other hand, attach only to the roots of the host plant and the aboveground morphology of the root hemiparasite is similar to strict autotrophs. Consequently, the hemiparasitic status of many species has only been discovered within the past 40 years. Most parasitic plants are hemiparasites (Atsatt 1983; Kuijt 1969) and attachment to a host is considered necessary for normal growth and reproduction in the wild (Gibson and Watkinson 1991; Kuijt 1969). However, there are documented cases of depauperate individuals of some annual hemiparasites completing their life history without a host (Seel and Press 1993). Many root hemiparasites have been grown to maturity without a host in a greenhouse with adequate water and nutrient additions (Seel et al. 1993; Atsatt and Strong 1970). The term "facultative" hemiparasite has been applied to species capable of autotrophic growth past the seedling stage, either in the wild or in culture. Obligate hemiparasites are those requiring a host for any growth to occur, including germination of the seeds,

which requires a chemical signal from the host root to initiate germination (Press et al. 1990). It should be noted that not all hemiparasites fall neatly into one of these two groups, and mode of nutrition could better be viewed as a continuum of dependence on a host, which may differ at various stages of life history (Kuijt 1969).

Root hemiparasites have been well studied over the past 40 years, especially annual root hemiparasites that utilize herbaceous hosts in open habitats (Gibson and Watkinson 1988; Atsatt and Strong 1970). There is little published information on the relationship between herbaceous, perennial root hemiparasites of woodlands and their arboreal hosts. We might expect the host-hemiparasite interactions to differ in these cases due to greater longevity of both species and the potentially great difference in size between host and parasite. Such size disparity could lessen the degree of harm suffered by the host or lessen the opportunity for light capture by the hemiparasite and thus its ability to be partially autotrophic.

Obligate hemiparasites generally have a narrow range of potential hosts, while facultative hemiparasites typically are capable of forming haustoria on a broad array of hosts (Pate et al. 1990; Watkinson and Gibson 1988; Musselman and Mann 1978; Kuijt 1969). The benefit derived from different host species can vary greatly, and in some cases, the degree of benefit provided by a host is positively related to the degree of harm it suffers when the hemiparasite is attached (Matthies 1996; Seel and Press 1993; Gibson and Watkinson 1991). Under field and greenhouse conditions, it has been demonstrated that the hemiparasite can selectively parasitize preferred hosts (Gibson and Watkinson 1992, 1991, 1989). Nitrogen-fixing legumes have been shown to be much more beneficial hosts than other species and to be competitively suppressed in grassland communities by the presence of certain hemiparasites (Gibson and Watkinson 1992). For root hemiparasites in the *Scrophulariaceae,* progress has been made in identifying species capable of serving as hosts; however, the degree of host selectivity is poorly understood (Watkinson and Gibson 1988). The host-hemiparasite relationship

has important fitness effects for each species, both within the context of the population biology of each and within the plant community as a whole.

It is generally accepted that hemiparasites are relatively inefficient in water use due to high rates of transpiration (Matthies 1995; Pate et al. 1990; Kuijt 1969). There is also evidence of nutrient use inefficiencies in the hemiparasite, and the total productivity per pot or field plot has been shown to be reduced when a hemiparasite is present (Matthies 1996, 1995; Watkinson and Gibson 1988). Higher rates of transpiration by the hemiparasite are thought to create the negative pressure necessary to draw water and solutes from the host (Seel et al. 1993; Kuijt 1969). Structural studies of haustoria of some root hemiparasites indicate the presence of xylem elements, but not phloem, in the haustoria, and the conventional wisdom has been that hemiparasites acquire mostly water and mineral elements from the host via a xylem bridge (discussed in Pate et al. 1990). Despite the lack of phloem in the haustoria several authors have reported transfer of carbon compounds from host to hemiparasite (Tennakoon and Pate 1996; Govier et al. 1967; Govier and Harper 1965). Other studies indicate that organic nitrogenous compounds are accessed by the hemiparasite (e.g., Seel and Press 1993) through connection to the xylem stream of the host. Solute transfer is apoplastic but the haustorium appears to play a role in regulating the solutes that enter the parasite (Press et al. 1990). There is speculation that the degree of benefit provided by a host depends on the solutes in the host xylem stream and the relative benefit of those solutes to the hemiparasite (Seel et al. 1993).

Nutrient status of the soil or growth medium can affect the host-hemiparasite relationship. Supplemental nutrients or rich soil can enable the hemiparasite to mature without a host. Gibson and Watkinson (1991) found that in rich soil the growth of the preferred host is less suppressed by the hemiparasite and the number of haustoria on that host is reduced relative to the nutrient poor treatment. In this same study, the hemiparasite formed more haustoria on the non-preferred host in rich soil compared to the nutrient-poor soil; thus it appears that the hemiparasite is less selective under

nutrient rich conditions. Studies of response of root hemiparasites to nutrient addition provide information about the relative functionality of the hemiparasite root system, which has been reported by some investigators to be poorly developed, lacking root hairs, and without mycorrhizal association (Seel et al. 1993; Kuijt 1969). Nutrient response studies also give an indication of the growth plasticity of a species in variable nutrient environments.

The host-hemiparasite relationship can be viewed as a function of: 1) the benefit gained by the hemiparasite from the host; 2) potential suppression of the host by the hemiparasite due to loss of water and solutes from the host vascular system; and 3) competition for common resources needed by each for autotrophic growth. Matthies (1995) investigated the effects of above and below ground interactions in growth of two hemiparasites and their leguminous host. He found that competition with the host for light reduced the shoot biomass of the hemiparasites by more than 30%, but the beneficial effects of the host were more than enough to offset this loss compared to growth without the host. To my knowledge this is the only study in which the balance between the parasitic and competitive aspects of the relationship has been explored. As mentioned previously, the degree of benefit from different hosts can be significant and this could reflect differing magnitudes of the numerator and denominator of the benefit/competition ratio with a given host.

This investigation focuses on the host-hemiparasite interactions of two herbaceous perennial hemiparasites of the family *Scrophulariaceae*, *Aureolaria patula* and *A. virginica*. Both species are reported to selectively parasitize oaks (Werth and Riopel 1979; Pennell 1935,1928). *Aureolaria patula* is a rare species endemic to slopes along a few river systems in Tennessee, southern Kentucky, and northern Georgia and Alabama. *Aureolaria virginica*, a more common congener, is widely distributed in dry open woods through the eastern U.S. and is ecologically similar to *A. patula*. Typically the flowering season for the two species does not overlap (*A. virginica* is completing anthesis in mid-August when *A. patula* begins to flower). Pollen from a late flowering

(browsed) stem of *A. virginica* was applied to stigmas of *A. patula* in 1997. Fruit set was 100% and viable hybrid offspring were produced (personal observation). This suggests the two *Aureolaria* species are relatively closely related. Because of similarity in habitat and close relationship, *A. virginica* is a reasonable comparison taxon for the investigation of host utilization of *A. patula*.

In this study I addressed these five questions: 1) Does *A. patula* grow less than *A. virginica* without a host under low nutrient conditions? 2) Does host species affect hemiparasite growth? 3) Are more haustoria formed on some host species than others? 4) Do root growth and shoot growth of the two hemiparasites differ in response to fertilization? 5) Do the combined effects of fertilization and host presence influence growth or root/shoot ratios? This dissertation provides the first published empirical information on host utilization by *A. patula*. In addition it is the first report of a comparison of host-hemiparasite interactions for a rare species and a common congener.

3.2 Methods

Three experiments were conducted in greenhouses during the normal growing season (April-October) for *A. patula* and *A. virginica*. Seeds of each species were collected from three to six populations in the wild in east Tennessee for three consecutive years (1995-1997). After collection the seeds were held dry at room temperature for 10-12 weeks. Seed germination procedures generally followed those described by King (1989) for *A. virginica*. Seeds were placed on paper in petri plates, moistened and cold stratified for 12 weeks prior to placement in the germination chamber (10 and 20°C alternating temperature coincident with 12 hr dark and light cycle). In the first experiment, the germinated seeds were transplanted directly into pots filled with crushed sandstone. Seedling mortality was high; consequently in the subsequent experiments germinated seeds were first transplanted into a peat-based growing mix and allowed to reach a two-leaf stage before transplanting into pots filled with sand. Sand was used as the growth medium because it can be rinsed off the root system with minimal damage to roots, thus allowing haustoria to remain intact. A small volume of

native soil was added to the growth medium in all experiments to allow mycorrhizal infection of the host trees and to provide consistency in microbial status of the growth medium.

Statistical analyses were performed using SPSS-PC, Version 8.0 (SPSS 1997). Some of the data were transformed prior to analysis to satisfy assumptions of normality within treatment combinations or of homogeneity of variance among treatment combinations. Specific transformations are identified for each response variable. In cases where the data could not be normalized, nonparametric tests were applied. Factorial ANOVA, least significant difference (LSD), and t-tests were used to test for statistically significant relationships.

Tables and figures show means of untransformed data. Figures are mostly boxplots, which illustrate the distribution of non-normally distributed data better than figures showing means and 95% confidence intervals. The interquartile range (25^{th} – 75^{th} percentile) is shown as a box with the median as a horizontal bar in the box, and lines extending from the box show locations of the largest and smallest values that are not outliers or extreme values.

3.2.1 White Oak Host – Fertilizer Experiment

This experiment evaluated early growth of *A. patula* and *A. virginica* seedlings with and without a host (half-sib white oak (*Quercus alba*) seedlings) under three fertilization regimes: 1) none (control); 2) low; and 3) high. The fertilizer was Sierra 17-6-10 Plus Minors Controlled Release, which is in pelletized form (see Appendix 5 for nutrient analysis). Initially five fertilization treatments were established (including a control) in a dilution series, with the highest level being the amount (16 g per gal. pot) recommended by the manufacturer (Sierra-Scotts) for ornamental greenhouse crops and each lower level being a 50% reduction by weight of the preceding level. The amount of fertilizer added to treatments 1 – 5 was 0, 2, 4, 8, and 16-g, respectively. After an extended period of hot weather, which caused rapid release of the pelletized fertilizer,

high mortality of the *Aureolaria* seedlings and oak in the two highest fertilization treatments occurred. Thus, the two higher fertilization treatments were eliminated from the experiment. The modified design of the experiment is shown in Table 3.1.

Table 3.1 Experimental design for White Oak Host - Fertilizer Response Experiment, with 10 replicates of each treatment combination for each species.

Treatment Combination	**A. patula**	**A. virginica**
Host – Control	10	10
Host – low fertilizer (2g)	10	10
Host –high fertilizer (4g)	10	10
No host – Control	10	10
No host – low fertilizer (2g)	10	10
No host – high fertilizer (4g)	10	10

In April 1996, *Aureolaria* seedlings of each species were assigned at random to one of six treatment combinations given in Table 3.1. In order to account for potential effects of light and temperature differences among greenhouse benches, treatments were arranged in a randomized block design. One of the five replicates of each treatment was randomly assigned to one of the five benches used in the study. Due to naturally low fertility of the growth medium (crushed sandstone), 275-ml of dilute liquid fertilizer (½ strength K Gro Best, a liquid fertilizer – see Appendix 5 for nutrient analysis) was added to all pots prior to planting of the *Aureolaria* seedlings. During the course of the experiment plants were watered to capacity two to three times each week and rotated periodically to avoid edge effects on the benches.

Under natural conditions *Aureolaria* seedlings form a rosette in the first season, with stem elongation occurring in the second year of growth or later. Many plants in the fertilization treatments developed an elongated stem during this one-year experiment. In these cases, stem height was recorded and 'rosette' diameter (plant foliage diameter) was measured as the distance from tip to tip of the longest leaf-pair on the stem. The

term 'rosette diameter' is meant to include diameter measurement on plants with an elongated stem. Final rosette diameters and stem heights were measured in mid-October 1996. Square root transformations of diameter data were made prior to ANOVA. Correlation coefficients (Spearman) for rosette diameter and stem height were calculated using untransformed data.

3.2.2 Host Suitability Experiment

Two trials were conducted to test host species suitability. The first included six tree species listed in Table 3.2. The second trial was initiated six-weeks after the first trial, when seedlings of two additional potential host trees, sweetgum (*Liquidambar styraciflua*) and red maple (*Acer rubra*), became available. White oak was included in both trials to provide a reference species for comparison of results.

3.2.2.1 Six Hosts Trial

Seedlings of *A. patula* and *A. virginica* were grown with six tree species (Table 3.2) under low nutrient conditions for two years to investigate which tree species are capable of serving as host and whether hemiparasite growth is better with some host species than others. The six species were selected based on availability and co-occurrence with

Table 3.2 Design of Host Suitability Experiment – Six Hosts Trial, with six replicates of each host - hemiparasite combination.

Host species	***A. patula***	***A. virginica***
Ironwood *Carpinus caroliniana*	6	6
Redbud *Cercis canadensis*	6	6
Dogwood *Cornus florida*	6	6
White oak *Quercus alba*	6	6
Red oak *Quercus rubra*	6	6
Post oak *Quercus stellata*	6	6

Aureolaria populations in the field (see Appendix 1). Several oak species were included to test the reported preference of *Aureolaria* for oaks as host tress (Werth and Riopel 1979; Pennell 1935, 1928). Two-year old tree seedlings were planted in gallon-size pots filled with sand approximately seven weeks prior to addition of the hemiparasite seedlings. Additional tree seedlings grown without a hemiparasite were included in the study to assess effects of the hemiparasites on the hosts. Seedlings of each *Aureolaria* species were assigned at random to each of the treatment combinations shown in Table 3.2.

One replicate of each treatment was selected at random and assigned to each of the five greenhouse benches used in the study; the sixth replicates were distributed evenly among the benches, as were the host trees without hemiparasites. Pots were periodically rotated on each bench to avoid location effects. Rosette diameters and stem heights were recorded during the first growing season. Plants were held in a 10° C greenhouse over the winter. At the end of the two-year period, diameters of the hosts were taken for comparison to initial diameters and sand was rinsed off the root systems in each pot. The number of haustoria was counted and roots of the host and hemiparasite were separated. Fine roots (<2mm) and coarse roots of the host were separated. Shoots and roots of the hemiparasites and roots of the hosts were dried at 75°C for at least one week prior to weighing. A $\log_{10}$ transformation was performed on shoot and root weights and number of haustoria prior to ANOVA.

3.2.2.2 Three Hosts Trial

The design of this trial was similar to the preceding one, except the three hosts, sweetgum, red maple and white oak, were grown on one greenhouse bench. Each treatment was replicated six times. Pots were rotated on the bench periodically. Plants were harvested and processed as described above. Shoot and root dry weights were transformed ($\log_{10}$ or ln) prior to ANOVA.

3.2.3 Redbud Host – Fertilizer Response Experiment

None of the *Aureolaria* in the White Oak Host – Fertilizer Response Experiment (Sect. 3.2.1) formed attachments to the roots of the host. The design was repeated in this experiment with several modifications: 1) quart-size pots were used rather than gallon pots to ensure greater contact between the root systems of host and hemiparasite; 2) redbud (*Cercis canadensis)* seedlings were selected to serve as the host; 3) only two fertilization treatments were included (no fertilizer and low level (¼ strength K Gro Best, a liquid fertilizer – see Appendix 5 for nutrient analysis)); and 4) each treatment was replicated 11 times. The experimental design is shown in Table 3.3.

Germinated seed were transplanted to a peat-based growing mix (Sunshine Mix, Sun Gro Horticulture Inc.; see Appendix 5 for composition) and allowed to grow for three weeks before transplanting to experimental pots. Half-sib redbud seedlings were grown for three weeks before the hemiparasites were added to the pots. During the experiment all plants were located on one greenhouse bench and rotated once a week to avoid position effects. Plants were watered to capacity every second day and dilute liquid fertilizer solution was applied weekly to the fertilization treatments; a comparable amount of water was added to the unfertilized treatments.

After 16 weeks of growth, plants were harvested for assessment of above and below-ground growth. Height of the hemiparasites and diameter of the host plants were

Table 3.3 Design of Redbud Host - Fertilizer Response Experiment, with 11 replicates of each treatment combination for each hemiparasite.

Treatment combination	***A. patula***	***A. virginica***
Host – Fertilized	11	11
Host – Unfertilized	11	11
No host – Fertilized	11	11
No host - Unfertilized	11	11

measured. Sand was rinsed off the root systems of all replicates using a stream of water and a trigger nozzle. The numbers of haustoria were counted and roots of the host and hemiparasite were separated. Roots and shoots of the hemiparasites and roots of the host were dried for one week at 75°C prior to weighing. Prior to ANOVA, shoot and root weight data were subjected to square root transformations, and the number of haustoria was $\log_{10}$ transformed.

3.3 Results

3.3.1 White Oak Host – Fertilizer Response Experiment

Aureolaria patula seedlings grew significantly larger than *A. virginica,* but presence of white oak had no effect on rosette size of either hemiparasite species (Fig. 3.1 and Table 3.4). Examination of the roots in pots containing a host and hemiparasite indicated no connection between the two root systems. With fertilization both hemiparasites showed a significant increase in size of the rosette relative to the controls (LSD, $P < 0.001$ for control compared to low and high fertilizer treatments) (Fig. 3.2). The response, however, was greater for *A. patula,* which accounts for the statistically significant interaction in Table 3.4. Increasing the level of fertilization from 2-g to 4-g per pot did not result in appreciable increase in size (Fig. 3.2). Both hemiparasite species were able to survive in nutrient-poor growing mix without fertilization or attachment to a host, but growth was minimal (rosette diameter < 45 mm).

Stem height of the hemiparasites was significantly correlated with rosette diameter ($r = 0.86$, $P = 0.001$, Spearman's correlation coefficient.). Few of the plants in the control treatments developed an elongated stem and, if so, the stem was short (<25mm). Presence of a host in the high fertilization treatment reduced stem height for both species, significantly for *A. patula* (Kruskal Wallis Test , $\chi^2 = 4.022$, 1 df, $P = 0.045$) (Fig. 3.3).

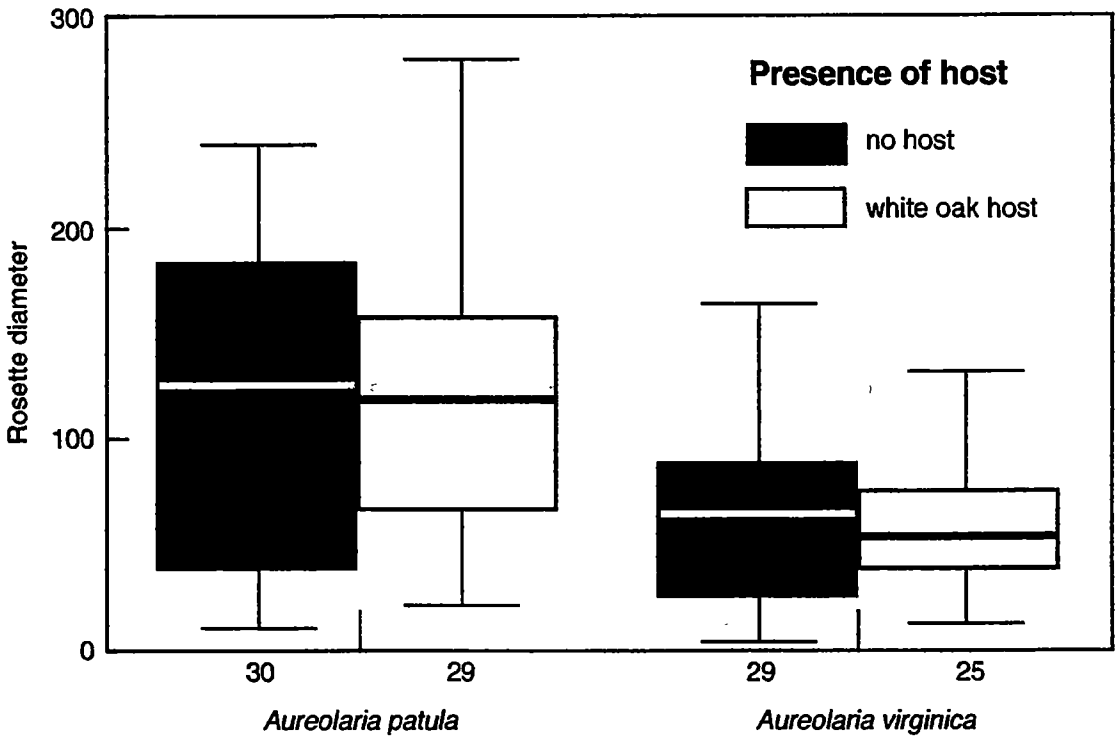


Fig. 3.1 Shoot growth (rosette diameter) of *A. patula* and *A. virginica* with and without a white oak host. *Aureolaria patula* grew significantly larger than *A. virginica*, but host presence had no effect on shoot growth of either species (ANOVA results in Table 3.4). Bar in each box is the median. N = number of plants.

Table 3.4 Comparison of two *Aureolaria* species, three levels of fertilization, and presence or absence of a host on *Aureolaria* rosette diameter in the White Oak Host – Fertilizer Response Experiment. ANOVA on square root transformations of rosette diameter. Effect of block (greenhouse bench) was not significant and, for simplicity, is not included in the table.

Source	df	F	Significance
Species	1	43.353	0.000
Fertilization	2	45.402	0.000
Host	1	0.070	0.792
Species * Fertil.	2	5.627	0.005
Species * Host	1	0.180	0.672
Fertil. * Host	2	1.436	0.243
Species * Fertil. * Host	2	0.214	0.808
Error	101		
Corrected Total	112		

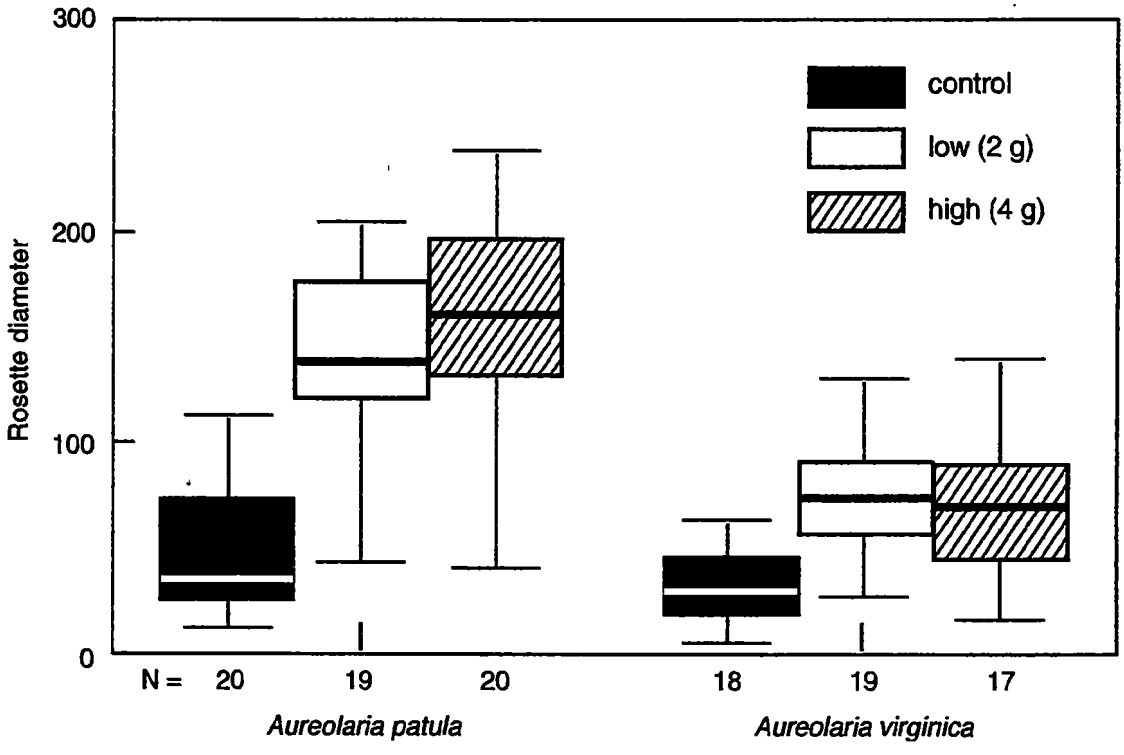


Fig. 3.2 Shoot growth (rosette diameter) of *A. patula* and *A. virginica* at three fertilizer levels. Fertilization increased growth for both species, but more for *A. patula* (ANOVA results in Table 3.4). Bar in each box is the median. N = number of plants.

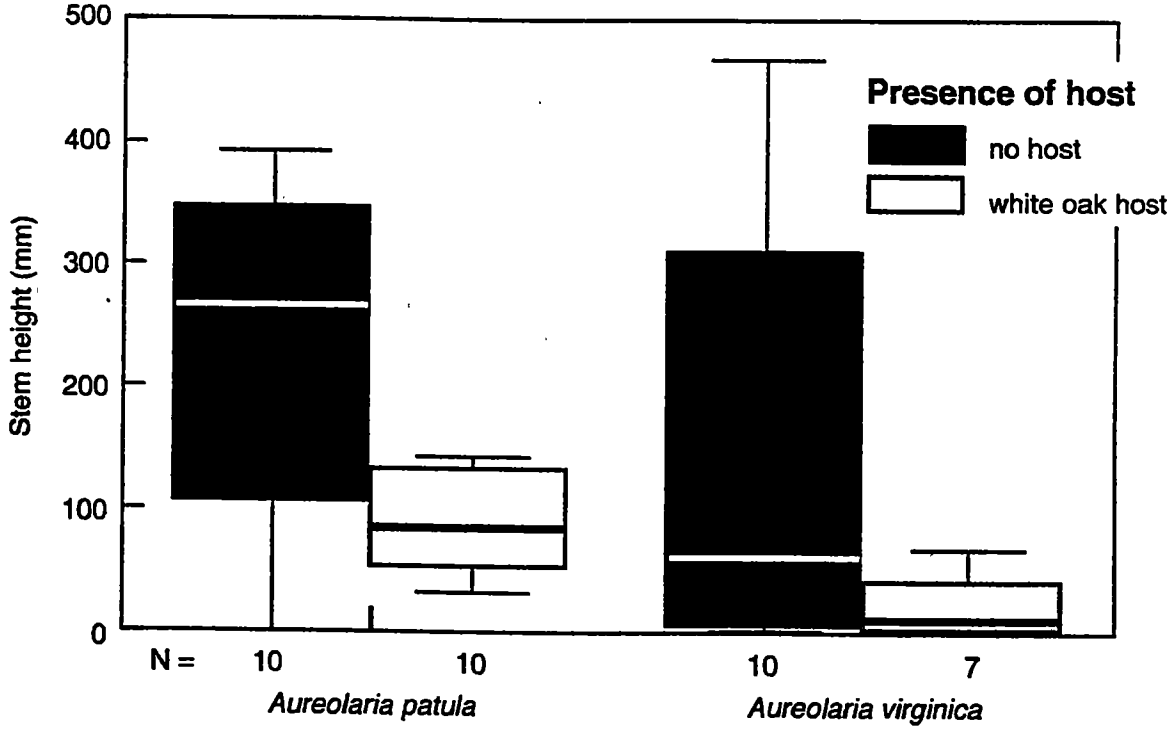


Fig. 3.3 Stem height of *A. patula* and *A. virginica* at the high (4 g) fertilization level in the presence of a white oak host. Stem height of *A. patula*, but not *A. virginica*, was significantly reduced in pots with a white oak host. Bar in each box is the median. N = number of plants.

3.3.2 Host Suitability Experiment

3.3.2.1 Six Hosts Trial

Aureolaria patula produced significantly more shoot and root biomass when attached to ironwood, red oak and dogwood than with the other three host species (Table 3.5 and Fig. 3.4). The relative ranking of host species in terms of benefit to shoot growth in *A. patula* was: ironwood ≅ red oak ≅ dogwood > redbud ≅ post oak ≅ white oak. Host species associated with significantly greater shoot growth in *A. virginica* were ironwood, redbud, and dogwood. The relative ranking of host species for *A. virginica* shoot growth was: ironwood > redbud ≅ dogwood ≅ red oak > post oak ≅ white oak. The two hemiparasites differed in total (shoot + root) biomass across hosts but these differences were not significant at the 0.05 level ($\log_{10}$ transformation, ANOVA, F = 3.318, 1/52 df, P = 0.076).

The interaction of hemiparasite species and host significantly affected total biomass (F = 3.230, 5/52 df, P = 0.015). The interaction can be attributed to the greater benefit of dogwood and red oak to *A. patula* compared to *A. virginica*. *Aureolaria patula* had significantly lower root/shoot ratios than *A. virginica* (ANOVA, F = 12.32, 1/52 df, P = 0.001,); host species was not a significant factor in these differences (F = 1.00, 5/52 df, P = 0.429). The interaction of hemiparasite species and host was not significant for root/shoot ratios (F = 1.912, 5/52 df, P = 0.113).

Survival was 100% for both hemiparasites growing with redbud and dogwood; survival with the other hosts was variable (Table 3.6). A comparison of survivorship of *A. patula* and *A. virginica* on each host indicates no significant differences between hemiparasites (Fisher's exact test values given in Table 3.6). Within each hemiparasite species, host was an important factor in seedling survival (Monte Carlo approximation of Fisher's exact test, based on 10,000 sampled tables, P = 0.076 for *A. patula* and P = 0.001 for *A. virginica*) (SPSS 1994). Another way to think of host suitability is in terms of the product of relative biomass X survival rate as a 'host suitability index'. Shown in

Table 3.5 Shoot and root growth of two *Aureolaria* species in pots with various hosts. Upper number in each table cell is mean dry wt.(g). Numbers of observations followed by standard deviations are in parentheses. ANOVA was performed on transformed (log_{10}) data. Means across rows with different letters are significantly different at 0.05 (post hoc comparisons, LSD, data file split by hemiparasite species). An "na" for standard deviation indicates only one survivor in that treatment.

	Ironwood	**Dogwood**	**Post oak**	**Red oak**	**Redbud**	**White oak**
A. patula	**5.85^{a}**	**1.91^{a}**	**0.22^{b}**	**3.22^{a}**	**0.34^{b}**	**0.03^{b}**
Shoot wt.	(3; 3.61)	(6; 1.04)	(5; 0.42)	(3; 3.03)	(6; 0.27)	(3; 0.02)
A. patula	**3.56^{a}**	**2.06^{a}**	**0.20^{c}**	**1.41^{ab}**	**0.45^{b}**	**0.04^{c}**
Root wt.	(3; 1.33)	(6; 1.52)	(5; 0.37)	(3; 0.60)	(6; 0.32)	(3; 0.06)
A. virginica	**0.64^{a}**	**0.26^{b}**	**0.07^{c}**	0.16	**0.30^{b}**	**0.06^{c}**
Shoot wt.	(6; 0.44)	(6; 0.11)	(4; 0.02)	(1; na)	(6; 0.21)	(3; 0.02)
A. virginica	**4.10^{a}**	**0.29^{b}**	**0.13^{b}**	0.21	**0.45^{b}**	**0.11^{b}**
Root wt.	(6; 5.41)	(6; 0.12)	(4; 0.07)	(1; na)	(6; 0.26)	(3; 0.05)

Table 3.6 Fraction surviving of *Aureolaria* seedlings grown with six host species. Values in significance column are Fisher's exact test for interspecific survivorship on each host, none of which were significantly different. NA indicates that all seedlings survived on that host. N = 6.

Host	***A. patula***	***A. virginica***	**Significance**
Ironwood	0.50	1.00	0.18
Dogwood	1.00	1.00	NA
Post oak	0.83	0.67	1.00
Red oak	0.50	0.17	0.54
Redbud	1.00	1.00	NA
White oak	0.50	0.50	1.00

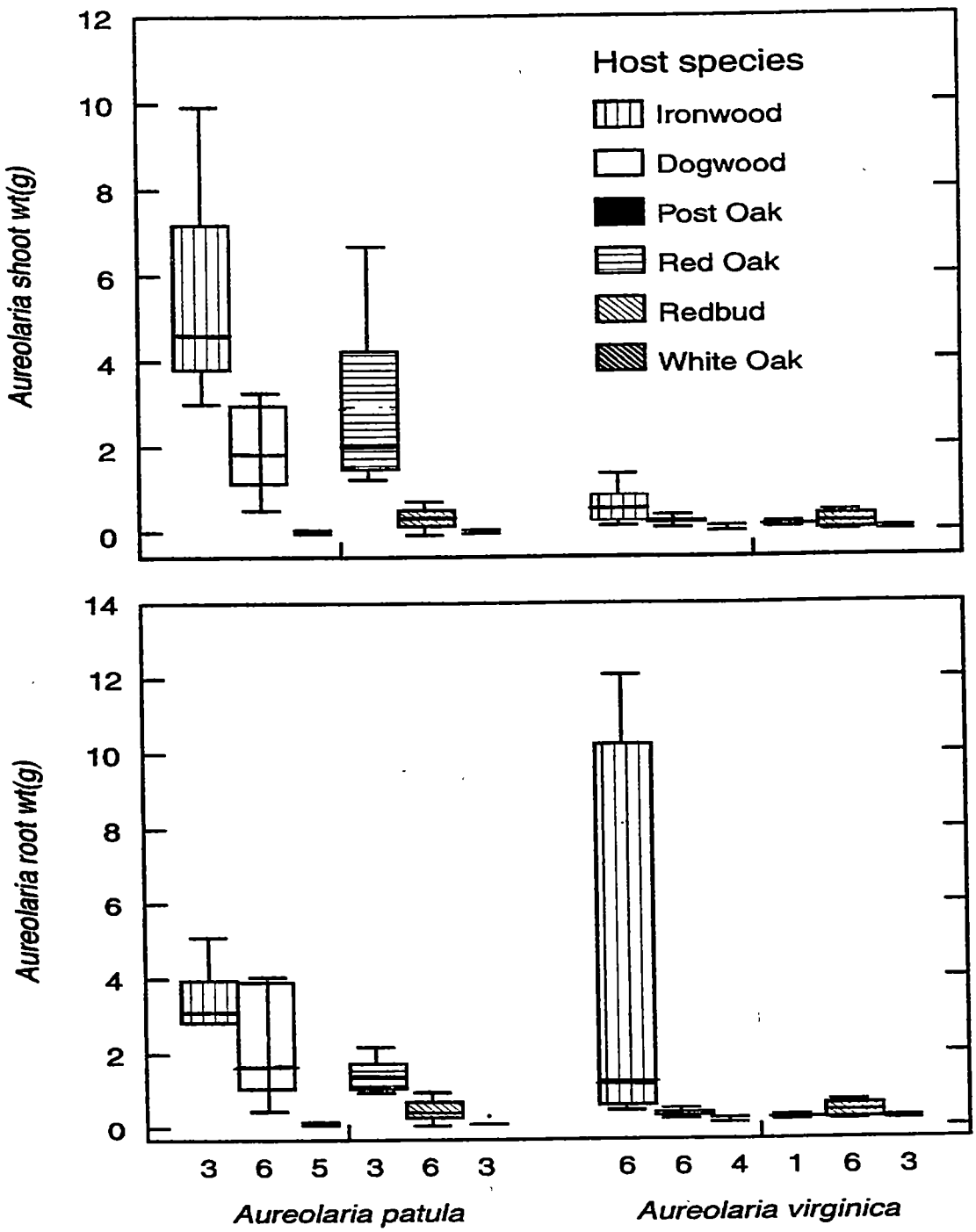


Fig. 3.4 Growth of shoots and roots of *A. patula* and *A. virginica*—six hosts (significantly different means in Table 3.5). For both species host was a significant factor in shoot and root growth. Ironwood was the most beneficial host for each species. Bar in each box is the median. N = number of plants.

Table 3.7 are values of this index considering relative shoot biomass and relative total biomass multiplied by the survival rates in Table 3.6. The relative ranking of the host species did not change from that indicated by mean shoot biomass alone. Nor was there a difference in host suitability index when either relative shoot biomass or relative total biomass was considered.

Neither presence of a hemiparasite nor hemiparasite species had an effect on growth of the host species (ANCOVA using initial host diameter as the covariate, $F = 3.74$, 2/94 df, $P = 0.331$). The host species did differ in growth but this effect was due to a higher relative growth rate of post oak compared to the other five species.

Host was a significant factor in the number of haustoria produced by the hemiparasites (ANOVA on $\log_{10}$ transformed data, $F = 16.64$, 5/50 df, $P < 0.001$) (Fig. 3.5). The hosts supporting the greatest hemiparasite biomass were parasitized more heavily. The

Table 3.7 Host suitability index: calculated as the product of relative biomass (by hemiparasite across hosts) and fraction of surviving seedlings for *A. patula* and *A. virginica* growing with six host trees. The higher values in the table indicate greater host suitability. The relative ranking of each host for each species does not differ whether shoot biomass alone or total biomass (root + shoot) are considered. The relative ranking of the hosts given by this index does not differ from the ranking assigned on the basis of mean absolute shoot growth.

	Ironwood	**Dogwood**	**Post oak**	**Red oak**	**Redbud**	**White oak**
A. patula						
Shoot	0.253	0.165	0.016	0.139	0.029	0.002
Total	0.243	0.216	0.018	0.115	0.044	0.002
A. virginica						
Shoot	0.430	0.174	0.031	0.018	0.201	0.020
Total	0.602	0.114	0.024	0.013	0.143	0.015

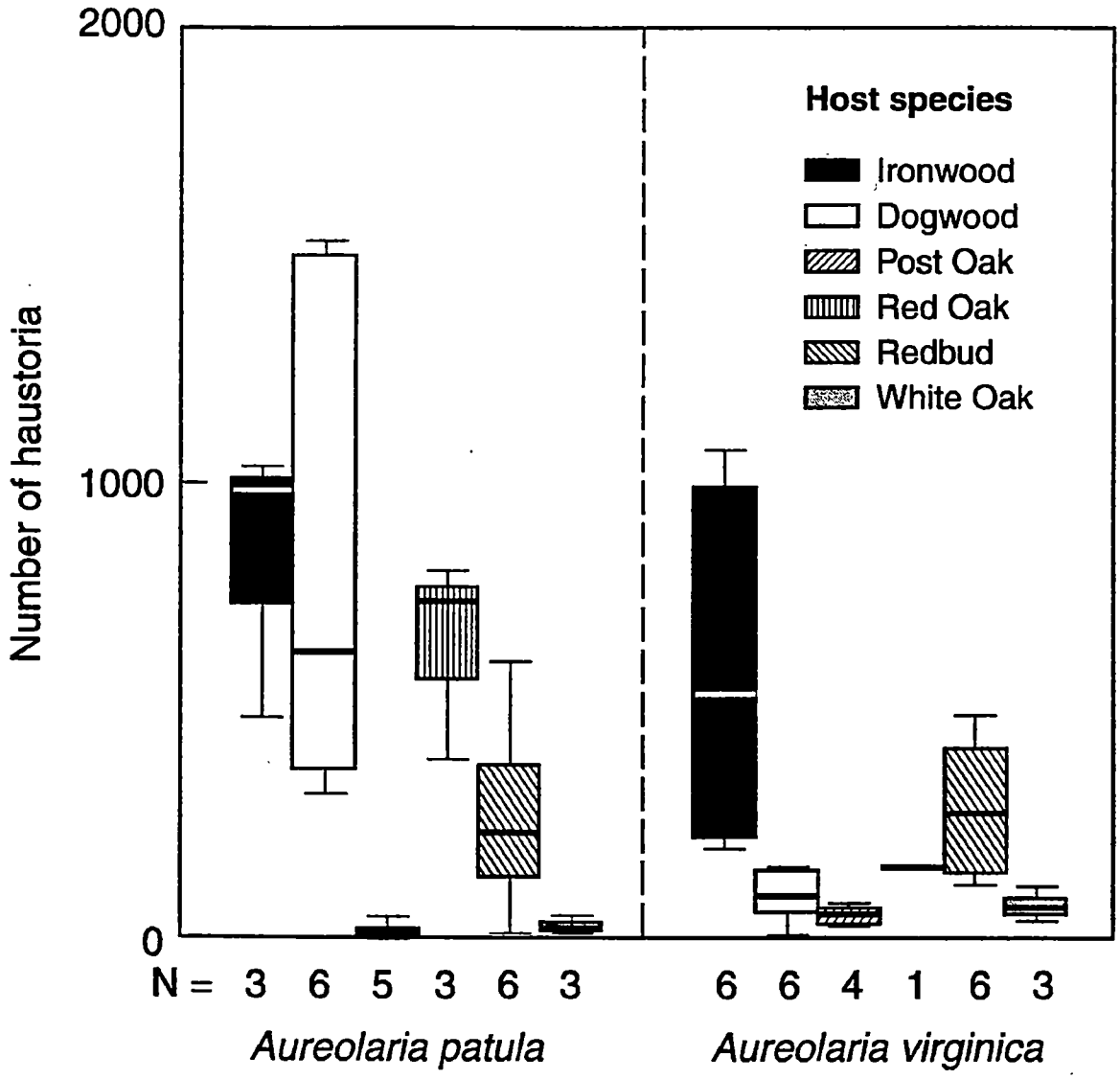


Fig. 3.5 Number of haustoria formed by *A. patula* and *A. virginica* on roots of six host species. Number of haustoria formed varied significantly with host. The two hemiparasites differed in number of haustoria on a given host for only dogwood and red oak, where *A. patula* produced significantly more haustoria than *A. virginica*. Bar in each box is the median. N = number of plants.

two hemiparasites differed in number of haustoria on a given host only on dogwood and red oak; *A. patula* produced significantly more haustoria than *A. virginica* (ANOVA, F = 25.95, 1/10 df , P = 0.001 and F = 23.74, 1/4 df, P = 0.017, respectively). Host species was a significant factor for both *A. patula* and *A. virginica* in the number of haustoria per unit of host fine root weight (Kruskal Wallis test, χ^2 = 14.33, 5 df, P = 0.014 for *A. patula* and χ^2 = 13.91, 5 df, P = 0.016 for *A. virginica*). Thus differences in number of haustoria by host are not an artifact of available host fine root. Number of haustoria was significantly correlated with hemiparasite shoot and root biomass (Pearson correlation coefficient on $\log_{10}$ transformed data, r = 0.82, P = 0.01 and r = 0.87, P = 0.01, respectively). Examination of the root systems of the hosts revealed that all host species were infected with mycorrhizal fungi (E. G. O'Neill, Oak Ridge National Laboratory, personal communication). This infection indicates that differences in mycorrhizal status of roots by species did not confound the issue of haustoria formation or hemiparasite growth on the six host species. There were many instances where the diameter of larger host roots (>2mm) was dramatically reduced distal to the attachment of haustoria. In these cases the haustoria also were typically larger than average.

3.3.2.2 Three Hosts Trial

Host and hemiparasite species and their interaction had significant effects on shoot biomass; only host species had a significant effect on root biomass (Fig. 3.6 and Table 3.8). *Aureolaria patula* grew larger than *A. virginica,* and sweetgum was a significantly more profitable host than white oak or red maple for both hemiparasites (post hoc tests, LSD, P < 0.001 in both cases). The significant interaction term for shoot biomass results from the very poor performance of *A. virginica* on red maple compared to *A. patula* (Fig. 3.6). Differences in root/shoot ratios between the species were attributable to near absence of root growth by A. *virginica* when growing in pots with red maple. Shoot growth of *A. virginica* on red maple was poor but root growth was more noticeably suppressed (Fig. 3.6).

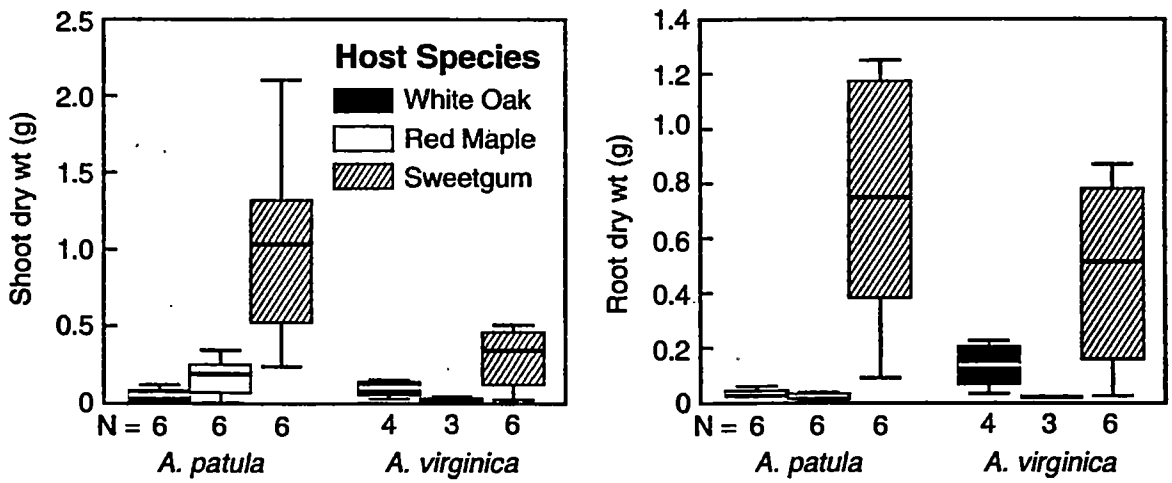


Fig. 3.6 Growth of shoots and roots of *A. patula* and *A. virginica*—three hosts (ANOVA results in Table 3.8). For both species, growth was greatest with sweetgum. Growth of *A. patula* was greater than *A. virginica* on sweetgum and red maple. Bar in each box is the median. N = number of plants.

Table 3.8 Comparison of the effects on shoot and root dry weights of *A. patula* and *A. virginica* growing with one of three host species (sweetgum, red maple and white oak). ANOVA on $\log_{10}$ (shoot) or ln (root) transformed data.

	Shoot dry wt.			Root dry wt.		
Source	**df**	**F**	**Sig.**	**df**	**F**	**Sig.**
Host	2	14.022	0.000	2	22.545	0.000
Species	1	5.769	0.024	1	0.164	0.689
Host * Species	2	3.844	0.035	2	2.450	0.107
Error	25			25		
Corrected Total	30			30		

3.3.3 Redbud Host – Fertilizer Response Experiment

Fertilized plants of *A. patula* and *A. virginica* grew significantly more than unfertilized plants both with and without a host (Table 3.9). Without fertilization, shoot and root weight of *A. patula* grown with a host did not differ from those grown without a host. For *A. virginica*, however, presence of redbud significantly depressed shoot and root growth in the unfertilized treatment. Shoot and root dry weight of both hemiparasites in the fertilization treatment were significantly less when redbud was present. For both hemiparasites the rank order of means by treatment combination for shoot and root biomass was: no host-fertilized > host-fertilized > no host-unfertilized > host-unfertilized. Significant differences in means are given in Table 3.9. Shoot and root growth were significantly suppressed in pots with redbud (Fig. 3.7).

Both hemiparasites formed haustoria on the roots of redbud. Both hemiparasite species and fertilization level were significant factors in number of haustoria (log10 [# haustoria + 10]) transformations, ANOVA, $F = 27.084$, 1/42 df, $P < 0.001$ and $F = 5.353$, 1/42 df, $P = 0.026$, respectively). A greater number of haustoria were formed in the fertilization treatments compared to the unfertilized treatments and by *A. patula* compared to *A. virginica* (Fig. 3.8). A few haustoria were observed on the roots of fertilized

Table 3.9 Treatment means for shoot and root final dry weights (g) for *A. patula* and *A. virginica* in Redbud Host – Fertilization Experiment. Standard deviations are given in parentheses. N = 11 for all cells. Means across rows with different letters are significantly different (t-tests on square root transformed data, $P < 0.05$).

	No host-fert.	**Host-fert.**	**No host-no fert.**	**Host-no fert.**
A. patula	**1.46**[a]	**0.71**[b]	**0.35**[c]	**0.26**[c]
Shoots	(0.48)	(0.35)	(0.13)	(0.18)
A. patula	**1.29**[a]	**0.58**[b]	**0.29**[c]	**0.23**[c]
Roots	(0.54)	(0.37)	(0.17)	(0.16)
A. virginica	**0.33**[a]	**0.18**[b]	**0.12**[c]	**0.06**[d]
Shoots	(0.18)	(0.07)	(0.07)	(0.04)
A. virginica	**0.38**[a]	**0.16**[b]	**0.11**[b]	**0.04**[c]
Roots	(0.17)	(0.07)	(0.06)	(0.04)

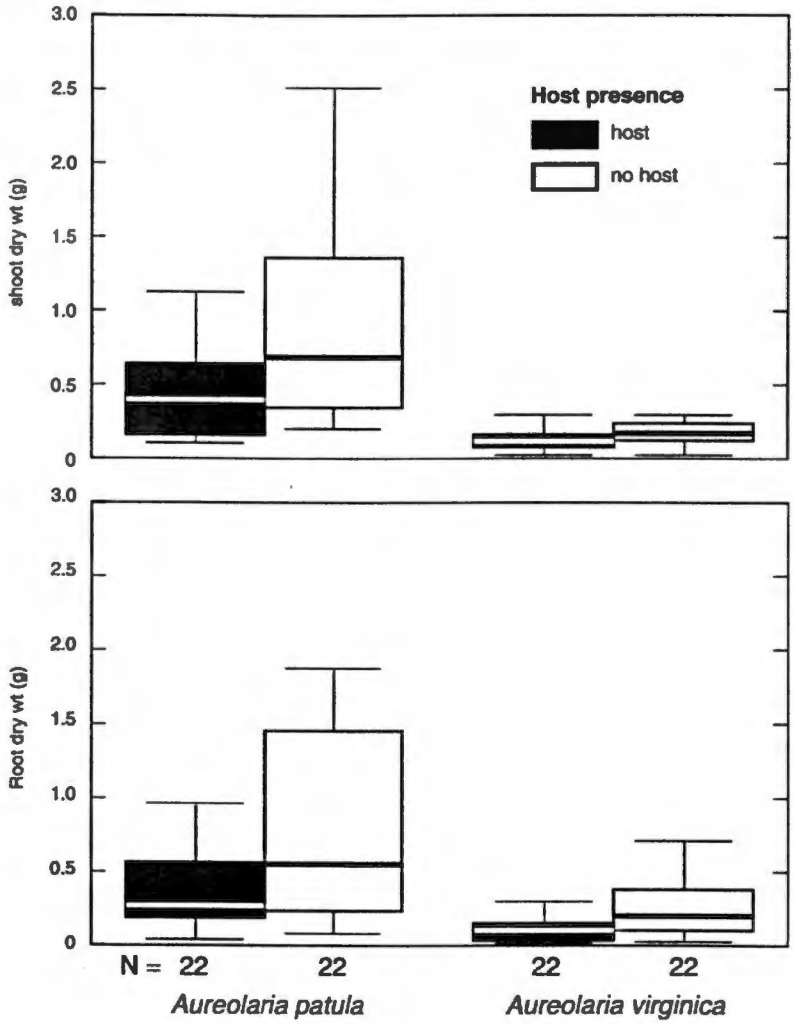


Fig. 3.7 Shoot and root growth of *A. patula* and *A. virginica* in response to presence or absence of redbud as a host. *Aureolaria patula* grew significantly larger than *A. virginica*, and growth of both hemiparasites was significantly suppressed in the presence of redbud. Bar in each box is the median. N = number of plants.

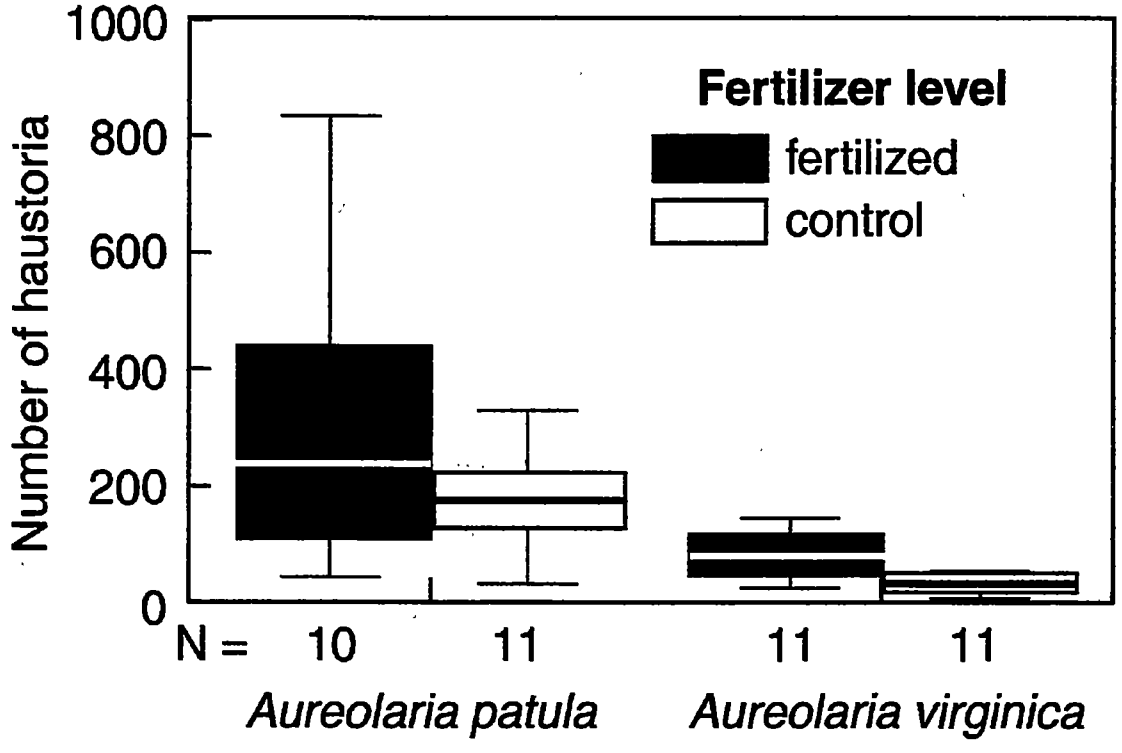


Fig. 3.8 Number of haustoria formed by *A. patula* and *A. virginica* on roots of redbud as a function of fertilization level. Fertilization increased the number of haustoria formed, and *A. patula* formed more haustoria than *A. virginica*. Bar in each box is the median. N = number of plants.

A. patula when no host was present (average 16 haustoria in five sampled root systems); *A. virginica* showed no evidence of self-parasitization in the absence of a host.

Although response to experimental treatments was generally similar for both hemiparasites, final dry weights of shoots and roots were less for *A. virginica* compared to *A. patula* (Fig. 3.7). Number of haustoria formed by *A. virginica* was less than for *A. patula* in both the control and fertilized treatments (Fig. 3.8). For both hemiparasites root/shoot ratios tended to be higher in the absence of redbud and root/shoot ratios of *A. virginica* were somewhat higher than for *A. patula.* However, neither of these differences was significant at the 0.05 level (t-tests, $t = -1.852$, 86 df, $P = 0.067$ and $t = -1.617$, 86 df, $P = 0.110$, respectively).

3.4 Discussion

All three greenhouse experiments indicate that *A. patula* achieves significantly greater size and biomass than *A. virginica* under most of the experimental conditions of this study. In the nutrient poor conditions of the White Oak Host – Fertilizer Response Experiment, however, the two species did not differ significantly in rosette diameter. Overall, the rare *A. patula* grows faster and to a greater size compared to *A. virginica*, a relatively common species. This result suggests that poor growth rate of individuals is not a factor in rarity of *A. patula.*

Both *A. patula* and *A. virginica* can survive without a host in nutrient-poor soil in the greenhouse if watered well, but growth is minimal. Under field conditions where competition and moisture stress occur, strict autotrophic growth is probably limited to seedlings from the time of germination until connection to a host during the first months of growth. Growth of *A. patula* and *A. virginica* did not significantly differ under low nutrient conditions, thus a lesser ability of seedlings to persist until they connect to a host is unlikely to be a contributing factor in rarity of *A. patula.* Ability to withstand water stress, which was not evaluated in this study, could be an important factor in

survival in the field. *Aureolaria patula* is often found in apparently xeric conditions, such as limestone bluffs, so if seedlings have greater susceptibility to moisture stress than *A. virginica*, then they must also have easy access to and attach relatively quickly to a host in xeric habitats.

Both hemiparasite species grew significantly more when nutrients were added to the growth medium, regardless of whether a host was present. A response to fertilization in the absence of a host indicates the presence of a functioning root system capable of water and mineral nutrient uptake. This capability has been reported for many facultative hemiparasites (Watkinson and Gibson 1988; Kuijt 1969). *Aureolaria patula* showed a greater growth response to fertilization than *A. virginica*. The greater growth response of *A. patula* to fertilization may indicate a more opportunistic response to favorable conditions or simply the physiological capability to better utilize mineral nutrients to enhance photosynthesis.

In light of the above, the lack of increased growth response to increased fertilizer level in the White Oak Host – Fertilizer Response Experiment is interesting. It may indicate that the plants were not capable of greater uptake or greater utilization of higher levels of mineral nutrients. Seel et al. (1993) found that the responsiveness of the hemiparasite *Rhinanthus minor* (Scrophulariaceae) to increasing levels of inorganic solutes was limited, both in pots in a greenhouse and in field plots. Light saturated rates of photosynthesis are typically much lower in hemiparasites not attached to a host (Seel and Press 1993). Thus the hemiparasites, none of which were attached to a host, may have been experiencing a bottleneck in growth related to low photosynthetic rate. Additional mineral nutrient availability would thus not result in an increase in growth.

The Host Suitability Experiment showed that although the hemiparasites formed haustoria on all hosts tested, the number of haustoria and the benefit provided to the hemiparasite varied widely. The host species most beneficial to the two hemiparasite species differed slightly. Based on shoot and root growth and number of haustoria, the

most beneficial hosts for *A. patula* were ironwood, red oak, and dogwood, the first two of which are dominants or codominants in the forest community at the four demographic study sites for *A. patula*. The hosts associated with greatest growth in *A. virginica* were ironwood, redbud, and dogwood. Field observations indicate that redbud and dogwood are common components of plant communities where *A. virginica* grows; however, ironwood, the most beneficial host of the three, typically does not co-occur with *A. virginica*. White oak and post oak were two of the least beneficial hosts for both hemiparasites, with biomass being up to two orders of magnitude less on white oak than biomass of plants growing with ironwood. White oak and post oak are representatives of the 'white oak' section of the genus *Quercus* and are reputed to be the favored hosts of the perennial *Aureolarias* (Werth and Riopel 1979; Pennell 1935, 1928). It is not clear whether small sample sizes in previous investigations or differing regional host utilization strategies are responsible for this inconsistency.

Although some hosts were clearly more beneficial than others, root/shoot ratios of plants in the Host Suitability Experiment did not differ by host. Thus, in contrast to reports for other hemiparasites (Matthies 1995), there is no evidence that *A. patula* or *A. virginica* reduced carbon allocation to the roots when attached to the more favorable hosts. Neither was growth of the more favorable hosts suppressed relative to the other hosts or to hosts growing without a hemiparasite present. This finding is a clear contrast to results previously reported for annual hemiparasites that dramatically suppressed growth of their most beneficial host (Matthies 1996, 1995; Gibson and Watkinson 1992, 1991).

For both hemiparasites, host species was a significant factor in seedling survival. Proximity to and attempts to parasitize some hosts is apparently of greater risk to the developing seedling. Seedlings survived best on dogwood and redbud, but those hosts did not lead to the greatest biomass accrual for each hemiparasite. Differential shading during the Host Suitability Experiment by some hosts is not considered a major factor because the greatest mortality occurred in pots with host species having no lower

branches (red oak and post oak). In addition, pots were rotated on the benches to prevent areas of greater shade and to allow all replicates to experience edge conditions (more light). It is possible that root exudates from some hosts, particularly oaks, inhibit growth of the hemiparasite seedlings. Oak trees can inhibit root growth of other species growing beneath them (Matizha and Dahl 1991) and decrease shoot growth and productivity of understory plants (Callaway et al. 1991; Gleissman 1978).

In the Redbud Host – Fertilizer Response Experiment, fertilization did not reduce the number of haustoria formed on the host compared to the unfertilized treatments. In fact there was a trend for larger hemiparasite root systems and greater numbers of haustoria in the fertilization treatments. A similar result was reported by Mann and Musselman (1981) for several species of *Aureolaria* and *Agalinis* grown in pots in a greenhouse. Root/shoot ratios of the hemiparasites also were not affected by fertilization, indicating no reduction in allocation of carbon to roots with fertilization. In the unfertilized treatments, root/shoot ratios were somewhat higher in the no-host treatments compared to those with a host, but these differences were not significant at the 0.05 level ($P = 0.065$). Matthies (1995) reported significant reduction in root allocation for two annual hemiparasitic Scrophulariaceae in the presence of a host. With larger sample sizes in the *Aureolaria* experiments, significant differences in root/shoot ratio may have been found. On the other hand, the differences in results could be related to an annual versus perennial life history. Over their lifetime perennials benefit from a greater investment in root system than annuals, which allocate only enough energy to root systems to sustain flower and seed production. Thus an annual hemiparasite receiving sufficient resources from a host would not be likely to invest further in roots.

The results of the Redbud Host – Fertilization Experiment raise some interesting issues concerning the host-hemiparasite relationship. Redbud decreased growth of the hemiparasites growing with them relative to autotrophic growth. The hemiparasites formed haustoria on redbud roots, but apparently the connection to the host vascular system was not beneficial enough to overcome other negative influences of the close

association. Perhaps competition for mineral resources or light between host and hemiparasite or biochemical defenses of the host dominated the interactions taking place under the conditions of the experiment. Clearly, with any host species the balance between competition and interaction beneficial to the hemiparasite over its life history must lean toward the latter or the strategy of hemiparasitism would be an evolutionary dead end. As shown in the Host Suitability Experiment and by other investigators (Matthies 1996, 1995; Watkinson and Gibson 1988; Atsatt and Strong 1970), there is a dramatically greater benefit associated with attachment to some hosts relative to others. Redbud appears to be a host that is on balance not beneficial to the hemiparasite under the environmental conditions of the Redbud Host – Fertilizer Experiment. Under field conditions where water stress is an important factor in growth, attachment to redbud may provide benefit in accessing moisture farther below ground surface. The benefit of attachment by a hemiparasite to deeply rooted hosts was demonstrated by Pate et al. (1990) for *Olax phyllanthi* in coastal heath of Australia. Both *Aureolaria* species in this study occur in dry forest edges or openings, often on rocky substrate that is subject to considerable water stress in late summer and fall. Ability to persist in these habitats during commonly occurring periods of drought could be a major benefit over the hemiparasite's lifetime and could make an association with a marginal host beneficial.

Other investigators have noted that some host species are clearly not beneficial to the hemiparasite attached to them. Yeo (1964) noted that some host species tested with several species of *Euphrasia* (Scrophulariaceae) suppressed growth of the hemiparasite. Occasional individuals were able to successfully utilize those hosts. It is not clear whether the beneficial interaction was due to different capabilities of the host or hemiparasite. Atsatt and Strong (1970) found that fecundity of the annual *Orthocarpus purpurascens* (Scrophulariaceae) was negatively affected by some hosts, including a nitrogen-fixing legume, *Trifolium ripens*. In addition, it was clear from their data that variability exists among individuals in ability to utilize a host. The authors suggest that populations of annual hemiparasites of grassland habitats may retain a degree of variability in autotrophic and heterotrophic capabilities, including host utilization

strategies, to be successful in an uncertain environment where reconnection between host and hemiparasite must be established annually. For perennial *Aureolaria* species, whose hosts are also perennial, such variability may not be a strong advantage. The present study was not designed to investigate individual host usage but rather the average benefit of a host to the species. Thus, although a particular host may be detrimental under greenhouse conditions relative to autotrophic growth, conditions in ecological time (e.g., annual drought) and in evolutionary time (e.g., variable host availability during landscape-level shifts in plant communities) may favor the ability to attach to hosts with only the potential to be beneficial.

In conclusion, some aspects of the host-hemiparasite relationship revealed by this investigation are different from those reported for annual hemiparasites attached to herbaceous hosts. In this study, there was no evidence of suppression of host growth by the hemiparasites, even for the hosts associated with greatest hemiparasite biomass. Reduced carbon allocation to hemiparasite root systems in the presence of a host did not occur. Significant depression of hemiparasite biomass in fertilized and unfertilized treatments was noted in the presence of redbud, a host well-parasitized by the hemiparasites. This result highlights the competitive aspects of host-hemiparasite interactions in a situation where the host is considerably larger than the hemiparasite and capable of detrimental shading as well as production of an arsenal of metabolites perhaps capable of chemical warfare (Callaway et al. 1991; Gleissman 1978). The hemiparasite seedling survival data also suggests that proximity to particular hosts may increase risk of hemiparasite mortality. Shading is especially troublesome for hemiparasite because it not only decreases light available for photosynthesis but also lowers transpiration rate. A relatively high transpiration rate is the means by which the hemiparasite draws solutes and water from the host.

The rare and common hemiparasite species differed in two main areas, total biomass accrual and preferred hosts. Overall, *Aureolaria patula* grew significantly larger than *A. virginica.* The list of best hosts for both hemiparasites included ironwood and

dogwood; *A. patula* grew equally well with red oak while *A. virginica* grew as well with redbud. Seedling survival, dependence on a host, and range of tree species utilized as hosts did not differ by hemiparasite species in this study. This indicates that, in general, the ability of *A. patula* to become established and connected to a host is not a factor limiting its abundance. Response to the most favorable hosts is more dramatic in *A. patula*; growth with the best host (ironwood) is up to 100 times greater than with the least beneficial host (white oak). The difference in growth is not so great for *A. virginica* (only 10 times greater). The canopy vegetation at four demographic study sites for *A. patula* in east Tennessee (Appendix 1) was dominated by tree species shown to be the most beneficial hosts of those tested. *Aureolaria patula* could be viewed as having a more risky life strategy – it grows very well in certain habitats where its preferred hosts are abundant, but its morphology and physiology render it less fit under "general" conditions. It grows rapidly in response to adequate water and nutrients and invests less in its own root system (*A. patula* has lower root/shoot ratios than *A. virginica*) and grows especially well on certain hosts. *Aureolaria virginica,* on the other hand, is more conservative in growth (has fewer and shorter stems, has smaller, thicker leaves and invests relatively more in its root system). Optimal edaphic conditions (limestone-derived soils and outcrops) and the distribution of the most beneficial hosts may limit *A. patula* to specific uncommon habitats along waterways.

Chapter 4. Investigation of Inbreeding Depression in a Small Population of *Aureolaria patula*

4.1 Introduction

Reproductive biology is an important component of population biology. Method of reproduction, mating system, fecundity, and establishment and survival of new individuals will heavily influence population stability over time. For species that reproduce exclusively by seeds, pollination biology, fecundity, germination, and establishment of seedlings are crucial to population dynamics. Because most seeds without specialized dispersal capabilities come to rest near the maternal plant (Waser and Price 1983) and pollen is primarily deposited on nearby plants (Thomson and Thomson 1989), genetic neighborhoods may exist within plant populations (Crawford 1982). In such cases a plant may receive a heavier dose of pollen from flowers on the same plant or close relatives, resulting in the potential for inbreeding depression in the offspring (Waser and Price 1989). Even if a species is self-incompatible, near-neighbor pollen may result in viable, but inbred, offspring.

Natural selection can remove less fit genotypes from the population through either pre- or post- fertilization selection events. Examples of pre-fertilization selection are pollen-style interactions and pollen competition. Pollen-style interactions include the inability of self-pollen to grow in the style, effectively preventing investment in offspring likely to suffer from inbreeding depression (Charlesworth and Charlesworth 1987). Pollen competition occurs when some pollen grains grow through the style faster than others and preemptively fuse with more eggs in the ovules or eggs in more favorable locations within the fruit (locations with better resource access or less likely to be aborted) (Quesada et al.1993). Post-fertilization selection may operate through ovule abortion related to early expression of lethal alleles or through unequal allocation of resources to more vigorous developing seeds. In some cases, there is evidence the maternal plant allocates more resources to either higher quality embryos (Mahy and Jacquemart 1999) or to selective embryo positions within the fruit (Vaughton and Ramsey 1997; Marshall and Ellstrand 1988). In other cases, it appears that resource

allocation to developing seeds differs due to the greater resource demand created by the most rapidly growing embryos, which are presumably the most fit (Lee and Bazzaz 1986; Lloyd 1980; Lloyd et al. 1980). This effect is probably mediated by plant hormones (Lloyd 1980). Post-fertilization selection may also occur after seed dispersal as weak genotypes in the seedling population are eliminated through intra- and interspecific competition.

Selective embryo abortion that is contingent on the genotype of the embryo, including maternal response to genetically inferior offspring, is considered natural selection. Differential provisioning of embryos by the maternal plant at the whole fruit level, rather than by individual embryo genotype, may be considered 'maternal effects' rather than natural selection. Increases in maternal provisioning to whole fruits have been shown as a response to the number of pollen tubes growing in the style (Marshall and Ellstrand 1986). In these cases, greater amounts of plant nutrients are available to the developing seeds as a result of physiological changes in the ovary after heavy or multiple-donor pollen treatments, and the resultant seedlings may be at an advantage in early growth. Charlesworth et al. (1987) suggest that these differences in maternal provisioning could account for differences in progeny fitness in multiple- versus single-donor crosses that have been attributed to natural selection via pollen competition.

It is difficult to distinguish among fitness enhancing processes operating prior to seed dispersal, even with experiments carefully designed to investigate each possibility (but see del Castillo 1998; Husband and Gurney 1998; and Cruzan and Thomson 1997). In theory, the processes of natural selection and differential maternal provisioning lead to different observations in mean offspring fitness (e.g., growth) and variability in fitness (Table 4.1, from Cruzan and Thomson 1997). If selection is occurring through pollen competition or selective embryo abortion, offspring from multiple-donor crosses are expected to have greater average fitness and less total variability in fitness than offspring from single-donor crosses. If maternal provisioning differences are occurring,

Table 4.1 Expected differences in mean offspring growth and phenotypic variance components under different models for the effects of single-donor and mixed (multiple)-donor pollen loads. From Cruzan and Thomson (1997).

Effect	Random processes	Maternal effects	Selection
Mean growth	single = mixed	single < mixed	single < mixed
Variance components			
Within fruit	single < mixed	single < mixed	single = mixed
Among fruit	single > mixed	single > mixed	single > mixed
Total	single = mixed	single = mixed	single > mixed

the expectation is for greater average offspring fitness but no difference in total variability in fitness from single- and multiple-donor crosses. Differences in within-fruit versus among-fruit variance components are also expected to differ with different effects models (Table 4.1). Of course, if neither selection nor maternal provisioning is a factor and pollination and embryo maturation are random processes, then we expect no difference in average fitness or total variance of offspring from single- and multiple-donor crosses. Thus, evaluation of average offspring growth and variability in offspring growth can provide clues to what processes are occurring prior to seed dispersal.

Bumblebees, which forage primarily in a near-neighbor pattern (Thomson and Thomson 1989), are reported to be the pollinators of *Aureolaria* species (Pennell 1935), and personal observations of *A. patula* support this. The present study was designed to determine whether inbreeding depression due to pollen deposition primarily among close neighbors is reducing fitness of seedlings and possibly contributing to small population size and rarity of *Aureolaria patula.* The approach was to look for evidence of reduced fitness in offspring resulting from open-pollinated flowers compared to those hand-outcrossed with a distant plant in the same population. Fischer and Matthies (1997) used this approach in a study of small populations of *Gentianella germanica*, a rare European species, and found evidence of inbreeding depression in progeny from

open-pollinations. The present study is preliminary, aimed at giving an indication of the mating system and the relative fitness of offspring (as reflected by early growth) produced in a small population (< 50 plants) of *A. patula*.

4.2 Methods

Seven plants of *A. patula* at the crest of Haw Ridge, a wooded limestone barren in Oak Ridge, TN, were used to compare seed set, germination, and early growth of seedlings resulting from hand-outcrossed, hand-selfed, and open-pollinated flowers. Inspection of flower buds revealed that anthers do not dehisce prior to anthesis. Flowers selected just prior to anthesis in early September 1997 received one of the following four treatments: 1) corolla and stamens were removed and pollen from a plant 30 meters away was applied to the stigma (hand-outcrossed); 2) corolla and stamens were removed and pollen from another flower on the same plant was applied to the stigma (selfed); 3) flower about to open was marked but not disturbed (open-pollinated); and 4) corolla and stamens were removed but no other manipulations were performed (to test whether removal of the corolla precludes pollinator visits and pollination). Each treatment was performed on one flower per plant. A single pollen donor was used for each of the hand-outcrossed treatments. Pollen was applied with a short section of monofilament fishing line. In the hand-crosses, pollen was applied in a manner that thoroughly coated the recipient stigmas. Maternal plants 1, 2 and 3 received pollen from the same donor, and plants 4 through 7 shared a different donor. Treated flowers were identified by a series of spots of "white-out" painted on the calyx tube.

Ripened fruits were collected in late October and held in paper bags at room temp for 3-4 weeks. Seeds were cold stratified in early December in petri dishes lined with moist filter paper and placed at 4°C. After 12 weeks seeds were germinated in a 10-20°C alternating temperature growth chamber under 12 hours of light coincident with the higher temperature. Seeds were transplanted when the cotyledons were emerged from the seed coat. Seedlings were planted in a greenhouse potting mix (ProMix BX) in liners of 36 cells per flat, with one seedling per cell. No host plants were present. The number of replicates per treatment ranged from 25 to 36 because one treatment had

lower seed set and some seedling mortality occurred in other treatments. All flats were placed on a greenhouse bench and rotated twice weekly to ensure all flats experienced environmental conditions at all locations on the bench. Seedlings were watered three times a week; no fertilizer was applied during the study. Shoot dry weights and stem elongation (bolting) were recorded at harvest (12 weeks after transplanting).

Statistical analyses were conducted using SPSS-PC (Ver. 8.0). Effects of maternal plant and pollination treatment on seed set, germination, and seedling dry weights were evaluated using ANOVA (general linear model, full factorial design). Phenotypic variance components in seedling dry weights were calculated using the Variance Components procedure; pollination treatment was a fixed factor and maternal plant was a random factor (SPSS Inc. 1994). The effects of maternal plant and pollination treatment on bolting of seedlings were evaluated using standard log-linear analysis for hierarchical models (SPSS Inc. 1997; Caswell 1989; Fingleton 1984).

4.3 Results

No fruits developed when flowers were self-pollinated; *A. patula* is apparently self-incompatible. No fruits developed for flowers whose corolla and stamens were removed but no pollen applied, confirming that pollinators did not visit flowers after the corolla was removed. For all other treatments, fruit set was 100%.

Seed set and seed germination did not differ between hand-outcrossed and open-pollinated treatments (Tables 4.2 and 4.3). Analysis of variance of seedling dry weights for the hand-outcrossed and open-pollinated treatments showed that both pollination treatment and maternal plant were significant sources of variation in seedling growth (Table 4.4). For all maternal plants, the open-pollinated treatments resulted in seedlings with higher average dry weight than the hand-outcrossed treatments (Fig. 4.1). There was no statistically significant interaction between factors (Table 4.4), indicating that all maternal plants responded in the same fashion to pollination treatment, although the magnitude of the response differed. Comparison of variance components showed that

Table 4.2 Seed production, germination, and percentage of resulting seedlings that bolted from open-pollinated (multiple pollen donors) and hand-outcrossed (single pollen donor) flowers of *A. patula*, Haw Ridge, Oak Ridge, TN, Fall 1997.

Parent ID	Pollination treatment	# of seeds per capsule	# germinating by 3/13/98[a]	Germination percentage	% seedlings bolting
1	Open	92	91	99	36.1
	Outcrossed	115	111	97	16.7
2	Open	98	87	89	2.8
	Outcrossed	78	60	77	5.6
3	Open	9[b]	9	100	0.0
	Outcrossed	129	118	91	2.9
4	Open	113	113	100	55.6
	Outcrossed	117	117	100	13.9
5	Open	26	25	96	16.7
	Outcrossed	100	100	100	0.0
6	Open	148	115	78	8.3
	Outcrossed	144	131	91	2.9
7	Open	125	82	66	0.0
	Outcrossed	108	91	84	0.0

[a] Seed collected 11-97; stored at 4°C starting 12-8-97; placed in a 10 and 20°C alternating temperature growth chamber on 3-3-98. No further germination after 3-13-98.

[b] Insect damage to this fruit; collected other open-pollinated fruits from this plant and used these as seedling source for inbreeding depression study.

Table 4.3 Test for effects of open-pollination versus hand-outcrossing (single-donor) on seed set and germination in seed from six maternal plants of *A. patula*. One maternal plant was omitted from the analysis because of insect damage to the fruit. Data were transformed prior to analysis using square-root and arcsine functions for seed set counts and germination percentages, respectively. Data are in Table 4.1.

Source	Sum of squares	df	Mean square	F	Signif.
Seed set					
Pollin.trt	1.469	1	1.469	0.607	0.471
Parent.id	23.676	5	4.735	1.958	0.239
Error	12.093	5	2.419		
Total	37.238	11			
Germination					
Pollin.trt	0.020	1	0.0197	0.806	0.410
Parent.id	0.829	5	0.1660	6.799	0.028
Error	0.122	5	0.0244		
Total	0.971	11			

Table 4.4 Analysis of variance for the effects of maternal plant and pollination treatment on final dry weight (mg) of offspring (12-week old seedlings).

Source	Sum of squares	df	Mean square	F	Signif.
Maternal plant	38293.3	6	6382.2	18.513	.000
Pollination trt	4388.0	1	4388.0	12.728	.000
Interaction	1774.6	6	295.8	0.858	.526
Error	163407.9	474	344.7		
Total	2184673.0	488			

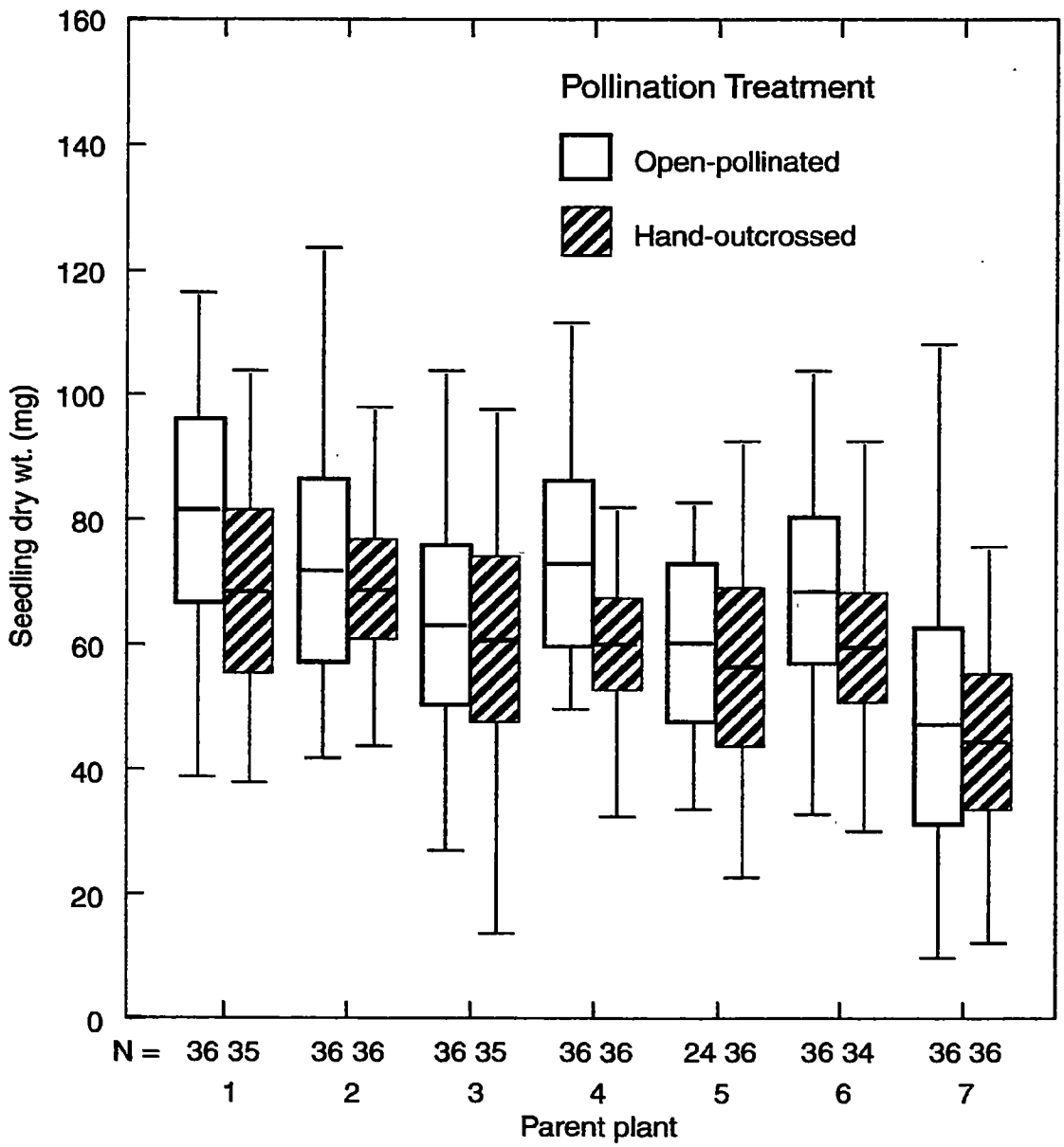


Fig. 4.1 Seedling dry weight of offspring from seven maternal plants of *A. patula* as a function of open-pollination or hand-outcrossing using a single pollen donor. Average dry weight of progeny from open-pollination are consistently higher than those from hand-outcrossing. Bar in each box is the median. N = number of plants in each treatment combination.

error or within parent variances (equivalent to within fruit variance in Table 4.1) were comparable for the two groups (single-donor = 346.93 and multiple-donor = 342.48). The among parent variances, the variability in mean seedling growth across maternal plants, (equivalent to among fruit variance in Table 4.1) for the single-donor crosses were lower (64.44) than for the multiple-donor crosses (103.87). Total variance was higher for the multiple-donor crosses (446.35) than for the single-donor crosses (411.37).

Log-linear analysis was used to test the null hypothesis that the probability of seedling bolting is independent of maternal plant and pollination treatment. The model that best fit the data included the effects of both factors on bolting but not their interaction. The probability of bolting was found to vary significantly among maternal plants (ΔG^2 = 76.8, 6 df, P <0.001) and was significantly greater for open-pollinated than hand-outcrossed flowers (ΔG^2= 15.1, 1 df, P <0.001) (Table 4.5).

4.4 Discussion

Aureolaria patula is apparently an obligate outcrosser. Self-incompatibility has been reported for other perennial species in the genus; hundreds of self-pollinations in five populations each of *A. laevigata* and *A. virginica* in southern Virginia resulted in no successful seed set (Bell and Musselman 1982). In the present study, however, only one population was investigated and degree of self-fertility has been shown to vary somewhat among populations of some "self-incompatible" species (Lipow et al. 1999). Additional populations would need to be investigated to be confident of the level of mating system variation in *A. patula*.

None of the indices of fitness measured in this study suggest that inbreeding depression is reducing overall fitness of progeny in the small population studied. The seed set and germination data give no evidence of differential abortion rate or reduction in germinability of offspring related to pollination treatment. The trend for open-pollinated progeny to grow larger than progeny from crosses with a single, distant

Table 4.5 Results of log-linear analysis of the effects of pollination treatment and maternal parent on bolting of the offspring. P is female plant (7 individuals), T is pollination treatment (open pollinated or outcrossed), and B is bolting (stem elongation or no stem elongation). ΔG^2 is the log likelihood ratio.

Model	df	ΔG^2	Signif.
PT, PB, TB	6		
PTB	0		
PTB	6	11.0	0.088[1]
PT, PB	7		
PT, PB, TB	6		
TB	1	17.4	0.000[2]
PT, TB	12		
PT, PB, TB	6		
PB	6	79.1	0.000[3]
PT, B	13		
PT, TB	12		
TB	1	15.1	0.000[2]
PT, B	13		
PT, PB	7		
PB	6	76.8	0.000[3]

[1] Probability the interaction effect of maternal parent and pollination treatment on bolting is zero.

[2] Probability the marginal and partial effect of pollination treatment on bolting is zero.

[3] Probability the marginal and partial effect of maternal parent on bolting is zero.

ollen donor implies that near-neighbor pollen exchange is not resulting in inbreeding depression. The somewhat greater probability of bolting in offspring from the open-pollinated treatment may also indicate higher fitness because these plants would be likely to flower earlier.

Hand-outcrossing using a single pollen donor resulted in a reduction in mean growth of offspring and lower total variability in growth of offspring relative to those from open-pollinated plants with multiple pollen donors (Table 4.6). This pattern does not fit the expectation that, if selection is occurring prior to seed dispersal, multiple pollen donors result in more fit and less variable offspring than those of a single-donor cross (Cruzan and Thompson 1997). Nor do the observed patterns fit what would be expected from the random effects model or the maternal effects model (Table 4.6). As Cruzan and Thomson (1997) indicate in their discussion of variance components, their model is a simplified concept of these processes. The actual genotypes of the pollen in multiple-donor crosses and greater variability in offspring from single donor crosses due to genetic segregation and recombination could confound the results. In spite of these

Table 4.6 Comparison of results from the present study with expected differences in mean offspring growth and phenotypic variance components shown in Table 4.1. The results of the present study do not fit the patterns for among fruit variance or total variance outlined in the conceptual model.

Conceptual Model of Cruzan and Thomson (1997)				
Effect	**Random**	**Maternal effects**	**Selection**	**Present study results**
Mean growth	single = mixed	single < mixed	single < mixed	single < mixed
Variance components				
Within fruit	single < mixed	single < mixed	single = mixed	single = mixed
Among fruit	single > mixed	single > mixed	single > mixed	single < mixed
Total	single = mixed	single = mixed	single > mixed	single < mixed

potentially confounding influences, Cruzan and Thomson (1997) hold the following expectation: in the absence of selection, the magnitude of within-fruit variance for the multiple-donor treatments should be substantially larger than the within-fruit variance for the single-donor treatment. The results of the present study are consistent with the natural selection effects model in two components: (1) greater average fitness of offspring from multiple-donor crosses, and (2) similar within-fruit variance components for the single- and multiple-donor treatments. The difference between my results and model expectations for the among-fruit variance components is interesting. The sample size of maternal plants in this study may be too small to detect the expected differences, or the conceptual model may need adjustment based on new data.

An alternate explanation for reduced mean growth of seedlings in the hand-outcrossed treatment is the effect of outbreeding depression, probably due to the disruption of locally adapted gene complexes. The pollen donor in the present study was 30-m distant from the maternal plant. An optimal outcrossing distance of 10 m was reported by Waser and Price (1989) for *Ipomopsis aggregata.* Outcrosses between plants in lesser proximity than 10-m resulted in reduced fitness in offspring, as reflected by seedling survival, probability of flowering, and timing of flowering. Crosses between plants over 100-m apart also resulted in reduced fitness. Fisher and Mathies (1998) found that outcrosses between plants of *Gentianella germanica* 10-m apart produced offspring of greater size than those from open-pollinations, outcrosses of plants 1-m apart, and inter-population crosses. These reports indicate that outbreeding depression in plants can occur in crosses over only moderate distances (greater than 10 m).

It is not possible from these data alone to say what processes occurred in the present study that resulted in significantly greater growth in offspring from open-pollinated multiple-donor crosses relative to crosses with a distant single pollen donor. The patterns of variability in offspring growth for the two treatments is not consistent with expectations of the conceptual model of Cruzan and Thomson (1997) for random effects, maternal effects, or natural selection. Without further work to test optimal

outcrossing distance, it is speculative to ascribe to outbreeding depression the reduction in offspring growth from single-donor crosses.

Despite this uncertainty the objective of this study has been met. Seed set, seed germination, and growth of seedlings resulting from natural pollinations in a small population of *A. patula* show no evidence of inbreeding depression. It is important to emphasize that the conditions of growth during this assessment do not mimic the natural environment. Moisture stress, as well as light and nutrient competition, could affect growth and survival of seedlings and reveal a different pattern of early growth response from that shown in this study.

Chapter 5. Summary and Conclusions

Rarity may be an aspect of a species' life history strategy, a strategy that results in scarcity but enables persistence. That strategy could be specialization for an uncommon habitat, such as the glade endemic, *Echinacea tennessensis*, or for habitat created by periodic disturbance, such as the specialization of *Pedicularis furbishii* for open patches created by ice scour along otherwise forested river banks (Menges 1990). Rarity may also be the consequence of external events such as human activity (e.g., habitat alteration or destruction or competition from introduced invasive species) or climate change (e.g., glacial relicts). There is often not a clear distinction between rarity related to life history strategy and rarity due to naturally occurring external events. Climate change may render some species rare because their habitat becomes uncommon. For example, Delcourt and Delcourt (1994) discuss the evidence from the fossil pollen record for the major expansion then decline in the distribution of *Ostrya/Carpinus* from 12,000 to 8,000 years before present (ybp). (*Ostrya virginiana* and *Carpinus caroliniana* are closely related taxa whose fossil pollen grains are morphologically indistinguishable.) The region of greatest past abundance of *Ostrya/Carpinus* is centered around the present-day distribution of *A. patula*. Therefore *A. patula* can be considered a relict of a post-glacial time period when disturbance was more frequent and seasonal contrast was greater (Delcourt and Delcourt 1994). These conditions may have promoted the occurrence of *Ostrya/Carpinus* and associated understory herbs, including *A. patula*.

What do the separate studies of *A. patula* reported in Chapters 2-4 suggest regarding its life history strategy and rarity? In Sect. 5.1 – 5.3, I summarize the results of the investigations on demography, host-hemiparasite interactions, and reproductive biology. I integrate the results of these studies in Sect. 5.4 as I draw conclusions on the life history strategy of *A. patula* and discuss landscape level patterns and processes that may be influencing its distribution and abundance.

5.1 Demography

Three of the four populations of *A. patula* studied in east Tennessee increased in size between 1995 and 1998. The fourth population (FP) decreased in size slightly due to mortality from flooding in 1998, but recruitment of new individuals the following year almost restored the number of plants. Population size alone is not a good indicator of population viability of perennial species. The frequency distribution of size classes and size-associated mortality and fecundity are crucial to population dynamics. I found increasing fecundity and decreasing mortality as plant size increased, which is a common pattern in woodland perennial herbs (Horvitz and Schemske 1995; Bierzychudek 1982). Reproductive values increased as plant size increased, with the largest size class, stage A3, having the highest value at all sites in all transition-years.

Plant dormancy was documented in three populations of *A. patula*. Tagged individuals were absent for a year (no aboveground presence) and then reappeared the next year. In only one case did a plant reemerge after a two-year absence. *Aureolaria patula* plants that do not reemerge after one year are not likely to do so, and I considered plants absent for two years to be dead. Plant dormancy was a more important component of population dynamics at some sites than others. No plants at GC were observed to reemerge after being absent. At the other three sites dormancy was not uncommon, especially at CR, where dormancy transitions were one of the crucial processes influencing λ.

The importance of dormancy in relation to catastrophic events was observed at the FP site, which was flooded for several months in late winter 1997 due to a beaver dam. Plants below the high water line died; *A. patula* cannot tolerate being underwater for multiple weeks. Many plants above the high water line emerged in the spring but the water level in the pond was then lowered rapidly due to dam removal, and an early season drought occurred. The soil at the site changed from very moist to dry over several weeks. All plants in the population became dormant for the rest of the season. Many reemerged the next season. This event and the population response to it may be a

clue to the strategy of *A. patula* under stressful conditions. Adult plants typically regress during dormancy (i.e., reemerge in a smaller size class, sometimes even as a juvenile), but it is survival nonetheless. Dormancy can be viewed as the response (or result) of individual plant circumstance or collectively as a population response to stressful environmental circumstances. Connection to a host is probably not a crucial component of this dynamic, because dormancy has been reported for other species that are not parasitic (Menges and Dolan 1998; Kephart and Paladino 1997; Lesica and Steele 1994; Mehroff 1989a, 1989b; Hutchings 1987).

Incorporating plant dormancy in matrix projection models is necessary to accurately portray population dynamics of some species. The model presented here for *A. patula* is the first report of explicit inclusion of dormant stages in a matrix model. In their comparison of plant demography using data on 66 species extracted from the literature, Silvertown et al. (1993, p. 467) considered dormancy in their generic composite demographic model. However, but I am not aware that dormancy of vegetative stages was explicitly incorporated in the matrix model for any of these 66 species.

Lambda values, as well as stage distributions, varied among sites and years. Thus it is not possible to identify a single pattern or trend for these demographic characteristics. However, evaluation of the elasticity matrices and λ values for each site X transition-year combination leads to some general statements on demographic trends. Populations at GC and CR have moderate growth elasticities, λ values above 1.0 in most years, and recruitment is occurring. The populations at GC and CR do not appear to be in decline. In contrast, the population at FZ, which exhibits low levels of fecundity, high dependence on survival of larger adult plants, and λ values near 1.0, could be a population in slow decline. The FP site in the 95-96 transition showed this same pattern, but after the flood in 1997, when a fresh layer of sediment was deposited, recruitment increased. One way to integrate these observations is to view the pattern evident at FZ as a way for the population to persist while "waiting " for conditions that favor recruitment and growth. If those conditions do not occur before the adult plants

senesce, the population will not persist. Population level dormancy could be viewed as an extreme form of this "survivalist" strategy.

The association between sites with 15-20% slopes (GC and CR) and relatively greater seedling recruitment deserves attention. I saw very few seedlings on level ground. Recruitment on slopes is far better. I expect that seedlings cannot get established in a heavy litter layer. Slopes keep leaf litter shallow and sheet erosion allows greater access to mineral soil.

Light is an interesting issue for *A. patula*. Clearly more light is better for growth and fruiting; plants in edge locations or in openings are larger and produce more fruits. But some populations seem to do well in shade (GC and other sites on private land that were not included in the demographic study). Occurrence of large plants in these populations is infrequent. Even in shady sites, edge locations are more favorable; large plants are not evident greater than 4 m away from the riverbank. At the few places away from the edge of rivers where I have seen *A. patula* growing, such as on top of Haw Ridge, the sites are dry and rocky with more open canopy than mesic woodlands.

5.2 Host-hemiparasite interactions

Greenhouse studies indicate that *A. patula* grows larger than *A. virginica*, its common congener, under most circumstances. Both hemiparasites can survive in nutrient-poor soil without a host, but growth is minimal. The unattached seedlings in poor soil have a normal morphology but remain small, i.e., in the left tail of the frequency distribution of normal rosette size. This is in contrast to some hemiparasites in the Scrophulariaceae, which initially grow in an abnormal "miniature" form until attachment to a host (e.g., *Tomanthera auriculata* (Cunningham 1990)). *Aureolaria patula* has a more dramatic response to fertilization than *A. virginica*; typically *A. patula* more than triples its biomass with fertilization. Both hemiparasites can form haustoria on a number of tree species, but some hosts are significantly more beneficial in terms of hemiparasite biomass than others. The most beneficial hosts for each species differed somewhat, but

two of the three best hosts were the same. For *A. patula* ironwood, red oak, and dogwood were the best hosts, and for *A. virginica*, ironwood, redbud, and dogwood were associated with greater growth. Host species had a significant effect on seedling survival. Some hosts were associated with higher seedling mortality. One of the most beneficial hosts for *A. patula*, red oak, proved to be most detrimental to *A. virginica* seedlings – only one out of six seedlings survived growing with red oak.

Growth response of *A. patula* to the most beneficial hosts was more dramatic than that of *A. virginica*, with up to an order of magnitude difference between growth of the hemiparasite species when grown with either the most or least beneficial hosts. The most heavily parasitized hosts were the most beneficial hosts for each hemiparasite. Not all available host species were well parasitized. For example, the hemiparasites produced few haustoria on white oak and red maple. Species in the white oak section of *Quercus* have been reported to be the favored hosts of perennial *Aureolaria* (Pennell 1928, 1934). I tested two oak species in that group (*Q. alba* and *Q. stellata*) and found them both to be poor hosts for each species.

Presence of a host, even one well parasitized by the hemiparasite, can suppress growth of that hemiparasite. This result has been reported for other hemiparasites in the Scrophulariaceae (Atsatt and Strong 1970). Redbud significantly suppressed growth of *A. patula* in the fertilization treatment only, but *A. virginica* was significantly suppressed by redbud in both the fertilization and control treatments. The hemiparasites did not suppress growth of their hosts, even the most beneficial hosts. Perennial woodland species of *Aureolaria* are apparently not important in shaping community structure and diversity the way open grassland hemiparasites have been shown to be (Gibson and Watkinson 1992).

Suppression of hemiparasite growth by a host could be related to several factors. As discussed in Chapter 3, hemiparasites appear to be limited in their growth response to greater mineral nutrient level in the soil. With fertilization, the host would be better

able to utilize available nutrients, grow larger and increasingly shade the hemiparasite. Increased shading slows autotrophic nutrition of the hemiparasite, as well as decreasing its transpiration rate, which is the mechanism for drawing nutrients from the host. Another mode of suppression of hemiparasite growth could be physiological incompatibility between host and hemiparasite. The chemical composition of materials drawn from the host vascular tissue has been suggested as the explanation for the difference in benefit gained from different hosts (Seel et al. 1993). The degree of benefit a hemiparasite derives from a host can be viewed as the net effect of: 1) gain from access to inorganic and organic compounds present in host vascular tissue; 2) energy loss due to reduction in auto-trophism resulting from shading by the host; 3) suppression of growth processes of the hemiparasite from inhibitory chemical compounds in the vascular tissue of the host and in exudate from the host roots; and 4) competition between host and hemiparasite for mineral nutrients in the soil. I expect the net benefit to a hemiparasite from attachment to different hosts is a continuum, and environmental conditions at a given time can shift the relative position of the relationship along the continuum.

The host-hemiparasite studies reported here are one of the few that focus on perennial, herbaceous hemiparasites attaching to the roots of trees. Most of the literature on host-hemiparasite interactions is focused on annual, grassland hemiparasites forming haustoria on the roots of herbaceous hosts (Watkinson and Gibson 1988). The relationships I have described for tree hosts and herbaceous hemiparasites, taxa with greatly differing biomass and competitive abilities regarding light capture, expand our knowledge of hemiparasitic relationships to woodland species. Knowledge of the degree of host suitability helps evaluate distribution of the hemiparasites in forested regions, and comparison of the interactions between a common and rare hemiparasite provides insight into potential differences in life history strategy that relate to rarity.

5.3 Reproductive biology

My observations of pollinator activity on *A. patula* are consistent with Pennell's (1928, 1935) reports that bumblebees are the primary pollinators of *Aureolaria*. Not all bees gained nectar in a way that facilitated pollen transfer. Specifically, I saw evidence of nectar robbing via small holes at the bases of the corollas. Bumblebees visiting *A. patula* flowers behaved in the way described by Thomson and Thomson (1989); they moved to the nearest open flower for a period of time and then flew to a farther location. Because the arched stems of *A. patula* become intermixed when plants grow close together, the nearest open flower may not be on the same plant as the previous flower.

The controlled crosses conducted in a small population of *A. patula* on Haw Ridge in Oak Ridge indicate that *A. patula* is not self-compatible. This is consistent with reports of self-incompatibility for other perennial species in the genus (Bell and Musselman 1982). Progeny from open-pollinations on seven maternal plants of *A. patula* consistently grew larger in a greenhouse than progeny from hand-outcrossing with a plant 30-m distant. The presumably greater deposition of pollen from near neighbors is apparently not leading to inbreeding depression. Additional studies will be necessary to determine if outbreeding depression contributed to reduced growth of progeny from hand outcrosses.

5.4 Conclusions

The goals of this research effort can be summarized by these three points: 1) to increase knowledge of the life history of *A. patula*, including the demographic structure of populations and the demographic processes crucial to population persistence; 2) to determine the relative benefit of different host species; and 3) to explore how the relationship between demographic processes, host-interactions, and reproductive biology might define the occurrence of *A. patula* on the regional landscape. The investigations I conducted were all at the scale of the individual or population. Thus extension to the landscape level is an extrapolation.

The life history of *A. patula* can now be more completely characterized. It is a relatively long-lived perennial, reproducing exclusively by sexual means. Flowers produced in late summer are pollinated by bumblebees, fruits mature and dehisce in late fall, and seeds are dispersed primarily by wind and gravity. Seeds are dormant at dispersal and germinate the following spring after winter stratification, or they lose viability during the following year. Seedlings remain in a rosette for one or more years, and subsequently produce one or two small, elongated non-reproductive stems. Under favorable environmental conditions in the field the seedling can advance quickly to reproductive size, from seed to flowering plant in three years. In the greenhouse, this transition could be accomplished in one to two years. *Aureolaria patula* plants are amazingly plastic in their growth transitions from year to year. Rapid advancements and dramatic regressions in size and dormancy are all possible. Regression in size is common after a year of dormancy. Larger plants live longer and produce more seeds than smaller plants. No single life stage appears to be most crucial to population growth and persistence across sites and years.

During seedling establishment in the field, the seedling root must connect to the roots of a host in order to grow to maturity (Kuijt 1969). My greenhouse studies indicate that seedlings in unfertilized soil without access to a beneficial host remain small. The progression from seedling to juvenile stage probably occurs as a consequence of attachment to a beneficial host. The host-hemiparasite studies in the greenhouse indicate that association with some hosts can suppress growth of the hemiparasite. Thus, at the population level, access to the roots of beneficial hosts is a crucial component of seedling recruitment. *Aureolaria patula* showed no evidence of greater requirement for a host in the seedling stage than *A. virginica*, but growth of *A. patula* in response to the more beneficial hosts was considerably greater at all stages of development.

Root hemiparasites primarily use their transpiration stream to access nutrients and water from the host (Press et al. 1990). Greater leaf area and greater water loss by the

hemiparasite increase access to nutrients in the vascular system of the host. Compared to *A. patula*, *A. virginica* has small leaves, with pubescence on the stem and leaves, both of which typically reduce water loss. Shoot morphology may partially explain why *A. virginica* does not grow in the areas where ironwood, the most beneficial host tested, is common. More light and heat may be required to drive the transpiration stream of *A. virginica* compared to *A. patula*, whose shoot morphology is that of a shade tolerant plant. I expect *A. patula* can transpire sufficiently in lower light situations to draw nutrients from the host. This would also explain why growth of *A. patula* is enhanced in lighter areas, such as edge locations.

Aureolaria patula can be viewed as having a more opportunistic life history strategy while *A.virginica* has the strategy of a generalist. *Aureolaria patula* can thrive only under a combination of conditions. These conditions include plant communities with a high density of the most beneficial hosts (e.g., ironwood and red oak), lack of herbaceous competitors which block light, proximity to a river or stream (for temperature moderation or fog or seed dispersal), and calcareous substrate. *Aureolaria patula* may have been more widespread 9,000 ybp when the environmental and vegetational conditions were more favorable (Delcourt and Delcourt 1994). Today it remains geographically restricted in range because its favored habitat is patchy and because self-incompatibility makes colonization of new sites by long distance seed dispersal less probable.

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Appendices

Appendix 1. Characterization of the Four Sites for Demographic Monitoring of *Aureolaria patula*, 1995-1998

A.1.1 Clinch River Site

Slope: 15%

Aspect: 20° south of west

Soils:

Depth: 11 samples ranged from 6 to 17 cm, average depth = 11cm

Textural Classification: loam, sand 31%, silt 48%, clay 21%

pH 6.5

Nutrient status: (ratings are based on agricultural soils)

total N- 511 ppm

P – 65 ppm (very high)

K – 96 ppm (low)

Ca – 5603 ppm (very high)

Mg – 73 ppm (medium)

Cation exchange capacity 31.8 meq/100g

Cation saturation: %K – 0.8; %Ca – 88.1; %Mg – 1.9; %H – 9.3

Brief description: This site is located on a moderately steep, rocky slope on the main channel of Clinch River, just upstream from the Pumping Station for water intake for the former Oak Ridge Gaseous Diffusion Plant (now called East Tennessee Technology Park) (Fig. 2.1), at approximate river mile 11.5. The site has abundant limestone outcrop and variable canopy closure – closed at the eastern end and open at the western end. *Yucca filamentosa* and *Rhus aromatica,* frequent shrubs of bluffs and dry rocky woods, occur at this site.

Table A.1.1 Canopy vegetation analysis for the Clinch River site. Diameter at breast height (dbh) was measured in centimeters for trees greater than 4-cm dbh. The sum of dbh for each species is used as an index of canopy cover. Density is number of occurrences in a 9-m X 25-m plot encompassing the area containing *A. patula*. Importance values are the sum of relative density and relative cover (range is 1- 200).

Species	Density (#/plot)	Relative density (%)	Σdbh (cm)	Relative cover (%)	Importance value
Ostrya virginiana	21	45.75	182	33.4	79.1
Juniperus virginiana	8	17.4	133	24.3	41.7
Quercus prinus	5	10.9	100	18.3	29.2
Carpinus caroliniana	6	13.0	42	7.7	20.7
Viburnum rufidulum	3	6.5	34	6.3	12.8
Quercus rubra	1	2.2	25	4.6	6.8
Acer saccharum	1	2.2	24	4.4	6.6
Cornus florida	1	2.2	6	1.0	3.2

A.1.2 Filtration Pond Site

Slope: 12%

Aspect: 70° west of south

Soils:

Depth: 15 samples ranged from 18 to >25 cm, average depth > 23 cm

Textural Classification: loam, sand 34%, silt 41%, clay 25%

pH 4.1

Nutrient status: (ratings are based on agricultural soils)

total N- 583 ppm

P – 36 ppm (optimum)

K – 106 ppm (medium)

Ca – 346 ppm (very low)

Mg – 69 ppm (medium)

Cation exchange capacity 9.1 meq/100g

Cation saturation: %K – 3.0; %Ca – 19.0; %Mg – 6.3; %H – 72.1

Brief description: This site includes a short slope rising from a level area adjacent to the Filtration Pond (on the Oak Ridge Reservation) at the 90° bend to the north in West Bear Creek Valley Road as it approaches the Clinch River (Fig. 2.1). Outfall from the pond drops through a culvert and enters the Clinch River at approximate river mile 14.5. No rock outcrops are visible. In 1995 this site had a closed canopy and the water level in the pond stayed nearly constant during wet seasons due to the outfall to the Clinch, which involves a drop of nearly 10 m. In late January 1997 the water level was extremely high, up 30 - 40 cm because of a beaver dam built at the metal grate covering the outfall. Water level was up 30-40 cm. The dam was removed, was soon rebuilt by the beaver, and was removed again. Water level thus fluctuated during the late winter and early spring. Plants above high water line began to break bud, but by early summer, when a drought occurred, all plants (except new seedlings) became dormant. The canopy was more open in 1997 and 1998 due to felling of trees by beaver. In 1999 stinging nettle (*Urtica dioica*) and japanese honeysuckle (*Lonicera japonica*) dominated the area along the water edge formerly occupied by *A. patula.*

Table A.1.2 Canopy vegetation analysis for the Filtration Pond site. Diameter at breast height (dbh) was measured in centimeters for trees greater than 4-cm dbh. The sum of dbh for each species is used as an index of canopy cover. Density is number of occurrences in a 9-m X 25-m plot encompassing the area containing *A. patula*. Importance values are the sum of relative density and relative cover (ranges 1 – 200).

Species	Density (#/plot)	Relative density (%)	Σdbh (cm)	Relative cover (%)	Importance value
Quercus rubra	8	19.5	261	36.3	55.8
Carpinus caroliniana	12	29.3	145	20.1	49.4
Liquidambar styraciflua	10	24.4	127	17.7	42.1
Carya tomentosa	2	4.9	52	7.2	12.1
Acer saccharum	3	7.3	25	3.4	10.7
Fraxinus pennsylvanica	2	4.9	26	3.6	8.5
Liriodendron tulipifera	1	2.4	43	6.0	8.4
Juniperus virginiana	1	2.4	16	2.2	4.6
Nyssa sylvatica	1	2.4	15	2.1	4.5
Prunus serotina	1	2.4	10	1.4	3.8

A.1.3 Frozen Head Site, Area A

Slope: 18 %

Aspect: 40° west of north

Soils:

Depth: 6 samples ranged from 5 to 36 cm, average depth 28 cm

Textural Classification: loam, sand 32%, silt 45%, clay 23%

pH 3.9

Nutrient status: (ratings are based on agricultural soils)

total N- 496 ppm

P – 26 ppm (medium)

K – 48 ppm (very low)

Ca – 266 ppm (very low)

Mg – 37 ppm (low)

Cation exchange capacity 7.4 meq/100g

Cation saturation: %K – 31.7; %Ca – 18.0; %Mg – 4.2; %H – 76.8

Brief description: The Frozen Head population is within the valley of Frozen Head State Park (Fig. 2.2), in two areas along Flat Fork Creek separated by approximately 100m. Area A is at a curve in Flat Fork Creek on a steep, wooded stream bank with open canopy, between the entrance road to Frozen Head Park and the Creek. The area encompassing *A. patula* is 5.5 m X 20 m.

Table A.1.3 Canopy vegetation analysis for Frozen Head, Area A. Diameter at breast height (dbh) was measured in centimeters for trees greater than 4-cm dbh. The sum of dbh for each species is used as an index of canopy cover. Density is number of occurrences in a 5.5-m X 25-m plot encompassing the area containing *A. patula*. Importance values are the sum of relative density and relative cover (ranges 1 – 200).

Species	Density (#/plot)	Relative density (%)	Σdbh (cm)	Relative cover (%)	Importance value
Quercus rubra	3	15	86	22	37.0
Liquidambar styraciflua	3	15	69	17.6	32.6
Juniperus virginiana	2	10	39	10.1	20.1
Liriodendron tulipifera	1	5	50	12.8	17.8
Diospyros virginiana	2	10	19	4.8	14.8
Acer rubrum	1	5	36	9.2	14.2
Platanus occidentalis	1	5	33	8.5	13.5
Tsuga canadensis	2	10	12	3.2	13.2
Carpinus caroliniana	2	10	8	2.1	12.1
Ulmus alata	1	5	28	7.1	12.1
Cornus florida	1	5	5	2.1	6.4
Morus rubra	1	5	4	1.1	6.1

A.1.4 Frozen Head Site, Area B

Slope: level

Aspect: NA

Soils:

Depth: 6 samples ranged from 15 to 36 cm, average depth 28 cm

Textural Classification: loam, sand 32%, silt 45%, clay 23%

pH 3.9

Nutrient status: (ratings are based on agricultural soils)

total N- 496 ppm

P – 26 ppm (medium)

K – 48 ppm (very low)

Ca – 266 ppm (very low)

Mg – 37 ppm (low)

Cation exchange capacity 7.4 meq/100g

Cation saturation: %K – 31.7; %Ca – 18.0; %Mg – 4.2; %H – 76.8

Brief description: Area B is on a level wide bench along Flat Fork Creek, about 100 m downstream of Area A. Area B is wooded, with a closed canopy. *A. patula* plants occur at edge of the woods near the Park road and into the woods about 8 m. Plants are largest at the edge of the woods and become increasingly smaller away from the edge. *Aureolaria patula* does not occur at streamside. Almost two-thirds of the canopy is represented by the four dominant trees: *Carpinus caroliniana, Liriodendron tulipifera, Cornus florida* and *Liquidambar styraciflua.*

Table A.1.4 Canopy vegetation analysis for Frozen Head, Area B. Diameter at breast height (dbh) was measured in centimeters for trees greater than 4-cm dbh. The sum of dbh for each species is used as an index of canopy cover. Density is number of occurrences in a 9-m X 25-m plot encompassing and exceeding the area containing *A. patula*. Importance values are the sum of relative density and relative cover (ranges from 1 – 200).

Species	Density (#/plot)	Relative density (%)	Σdbh (cm)	Relative cover (%)	Importance value
Carpinus caroliniana	11	24.4	110	19.2	43.6
Liriodendron tulipifera	7	15.6	132	23.1	38.7
Cornus florida	6	13.3	60	10.5	23.8
Liquidambar styraciflua	4	8.9	62	10.8	19.7
Oxydendrum arboreum	3	6.7	34	5.9	12.6
Tsuga canadensis	3	6.7	29	5.0	11.7
Pinus echinata	1	2.2	39	6.8	9.0
Juniperus virginiana	1	2.2	37	6.5	8.7
Acer saccharum	2	4.4	14	2.4	6.8
Prunus serotina	2	4.4	13	2.3	6.7
Platanus occidentalis	1	2.2	20	3.4	5.6
Carya sp.	1	2.2	8	1.4	3.9
Nyssa sylvatica	1	2.2	6	1.1	3.3
Fagus grandiflora	1	2.2	5	0.9	3.1
Quercus velutina	1	2.2	4	0.7	2.9

A.1.5 Grassy Creek Site

Slope: 16%

Aspect: 40° west of north

Soils:

Depth: 10 samples ranged from 5 to 25 cm, average depth 12 cm

Textural Classification: silty loam, sand 27%, silt 54%, clay 19%

pH 4.1

Nutrient status: (ratings are based on agricultural soils)

total N- 421 ppm

P – 29 ppm (medium)

K – 74 ppm (low)

Ca – 419 ppm (very low)

Mg – 88 ppm (medium)

Cation exchange capacity 8.2 meq/100g

Cation saturation: %K – 2.3; %Ca – 25.5; %Mg – 8.9; %H – 63.4

Brief description: This site is on a north-facing, moderately steep slope along the Grassy Creek embayment of the Clinch River, on TVA-owned property (Fig. 2.1). The embayment is separated from the main channel by an earthen berm supporting an access road; a large culvert connects the two bodies of water. Outflow from Grassy Creek enters the Clinch River approximately at river mile 14.6. Some limestone outcrop is evident at the site. A relatively diverse second –growth forest grows at the site. Seventy-three percent of the canopy is comprised of three dominant trees: *Carpinus caroliniana, Ostrya virginiana,* and *Quercus rubra.*

Table A.1.5 Canopy vegetation analysis for the Grassy Creek site. Diameter at breast height (dbh) was measured in centimeters for trees greater than 4-cm dbh. The sum of dbh for each species is used as an index of canopy cover. Density is number of occurrences in a 9-m X 25-m plot encompassing and exceeding the area containing *A. patula*. Importance values are the sum of relative density and relative cover (ranges 1 – 200).

Species	Density (#/plot)	Relative density (%)	Σdbh (cm)	Relative cover (%)	Importance value
Carpinus caroliniana	18	42.9%	283	39.4	82.3%
Ostrya virginiana	6	14.3	90	12.6	26.9
Quercus rubra	1	2.4	148	20.6	23.0
Liquidambar styraciflua	3	7.1	54	7.5	14.6
Liriodendron tulipifera	2	4.8	58	8.1	12.9
Fagus grandiflora	3	7.1	16	2.2	9.3
Aesculus octandra	3	7.1	15	1.9	9.0
Diospyros virginiana	1	2.4	20	2.8	5.2
Quercus primus	1	2.4	14	1.9	4.3
Fraxinus pennsylvanica	1	2.4	5	0.7	3.1
Acer saccharum	1	2.4	4	0.6	3.0
Ulmus alata	1	2.4	4	0.6	3.0

Appendix 2. Field Data for Individual Plants at Each of the Four Sites for Each of the Four Years.

This appendix has four multi-page tables, one for each of the four sites. The column headings in these tables are as follows:

Plant ID — The tag number for the individual plant

Data from Fall 1995 in the next four columns

- Stem95 — Number of stems
- Area95 — Basal area of the plant (mm), calculated as product of number of stems and average diameter of the five largest stems. Recorded as zero for seedlings.
- Fruits95 — Total number of fruits on five randomly chosen stems
- Stage95 — Demographic stage assigned to the plant. See Sect. 2.5.1 for description of stage categories.

Data from Fall 1996 in the next four columns, and data from Fall 1997 in the following four columns. Definitions are the same as for 1995.

Data from Fall 1998 in the final three columns. Fruits were not counted in 1998.

Table A.2.1. Data for individual plants at the Clinch River site for 1995, 1996, 1997, and 1998.

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
1	14	123.8	1207	A3	38	323.0	2402	A3	24	210.2	499	A3	35	217.0	A3
1A				A3dor	16	82.2	250	A3	15	106.8	0	A3	7	32.2	A2
2	29	212.9	563	A3	57	389.9	1174	A3	41	247.6	426	A3	45	180.0	A3
2A								A1dor	2	4.4	0	A1	1	3.0	NR
2C												A3dor	16	67.2	A3
3	2	13.3	90	A1	0	0.0	0	D	0	0.0	0	D	0	0.0	D
3B												Sd	1	4.0	NR
3C												Sd	2	6.0	NR
3D												Sd	2	6.0	NR
3E												A2dor	6	15.6	A2
4A	2	8.0	28	A1	3	13.9	33	A1	0	0.0	0	D	0	0.0	D
4B	4	NA	0	A1	7	18.6	0	A2	0	0.0	0	A2dor	3	7.0	A1
4C				A1dor	3	9.1	0	A1	5	19.8	16	A2	0	0.0	D
4D				A1dor	6	14.5	0	A1	1	3.3	0	NR	9	30.6	A2
4E								Sd	1	2.1	0	NR	2	4.0	NR
4F								Sd	1	3.1	0	NR	0	0.0	D
4G								A1dor	2	2.6	0	A1	2	5.0	NR
4H								Sd	1	3.0	0	NR	2	6.0	NR
4I												Sd	1	2.0	NR
4J												Sd	2	4.0	NR
4K												Sd	1	3.0	NR
4L												Sd	2	2.0	NR
4M												Sd	2	6.0	NR
4N												A1dor	3	11.0	A1
4P												Sd	1	2.0	NR
4Q												Sd	2	2.0	NR
5	4	17.2	61	A2	0	0.0	0	D	0	0.0	0	D	0	0.0	D
6	16	109.4	323	A3	10	52.4	144	A2	14	66.6	252	A3	18	75.6	A3
6B												A1dor	5	15.0	A1
6C												Sd	2	6.0	NR
6D												Sd	2	4.0	NR

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
6E												Sd	1	3.0	NR
7	1	3.9	1	NR	0	0.0	0	D	0	0.0	0	D	0	0.0	D
8	3	17.1	66	A2	3	12.0	89	A1	0	0.0	0	D	0	0.0	D
9	4	18.1	156	A2	6	28.8	0	A2	7	32.8	110	A2	3	11.0	A1
10	1	4.7	6	NR	0	0.0	0	D	0	0.0	0	D	0	0.0	D
11	6	25.3	0	A2	21	71.8	0	A3	10	39.0	0	A2	23	69.0	A3
11B												Sd	1	2.0	NR
11C												Sd	2	4.0	NR
12A	4	17.5	0	A2	8	27.7	0	A2	8	33.3	0	A2	11	46.2	A2
12B	5	NA	0	A1	1	1.3	0	NR	0	0.0	0	NRdor	2	2.0	NR
12C				A1dor	2	2.2	0	A1	0	0.0	0	D	0	0.0	D
12D												Sd	3	4.0	NR
13	3	8.5	0	A1	6	12.8	0	A1	0	0.0	0	A1dor	3	8.0	A1
14	1	2.5	0	NR	1	1.6	0	NR	0	0.0	0	NRdor	1	1.0	NR
14A									1	0.0	0	Sd	0	0.0	D
15A	2	4.0	0	A1	7	18.5	0	A2	3	11.0	0	A1	3	9.0	A1
15B	1	NA	0	Sd	0	0.0	0	D	0	0.0	0	D	0	0.0	D
15C								Sd	2	4.1	0	NR	1	1.0	NR
16A	2	2.8	0	A1	2	3.9	0	A1	2	3.7	0	NR	3	6.0	NR
16B				Sd	1	0.5	0	NR	0	0.0	0	D	0	0.0	D
16C				Sd	1	1.8	0	NR	0	0.0	0	D	0	0.0	D
16D												Sd	1	1.0	NR
16E												Sd	3	5.0	NR
17A	1	1.3	0	NR	3	6.3	0	A1	2	3.8	0	NR	3	5.0	NR
17B				A1dor	3	10.2	0	A1	1	6.5	0	A1	2	4.0	NR
17C				Sd	1	1.0	0	NR	0	0.0	0	NRdor	2	4.0	NR
17D								Sd	1	3.3	0	NR	2	5.0	NR
17E								Sd	1	2.2	0	NR	1	4.0	NR
18	22	81.4	59	A3	29	154.3	52	A3	0	0.0	0	D	0	0.0	D
19A	1	4.4	0	NR	0	0.0	0	J1dor	1	2.7	0	NR	3	8.0	A1
19B	8	NA	0	A2	7	NA	0	A2	0	0.0	0	A2dor	3	6.0	NR
20	4	5.7	0	NR	1	2.2	0	NR	0	0.0	0	D	0	0.0	D

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
20B												Sd	1	2.0	NR
21	1	3.2	0	NR	2	4.0	0	A1	0	0.0	0	D	0	0.0	D
22	1	2.6	3	NR	1	1.9	0	NR	0	0.0	0	D	0	0.0	D
22B												Sd	1	5.0	NR
23	2	14.6	32	A1	16	69.1	16	A3	1	3.3	0	NR	0	0.0	D
24A	3	8.9	6	A1	5	21.5	0	A2	13	51.2	104	A2	11	39.6	A2
24B				A1dor	2	2.0	0	A1	1	1.9	0	NR	1	2.0	NR
24C												Sd	1	1.0	NR
24D												A1dor	3	9.0	A1
24E												Sd	2	4.0	NR
24F												Sd	1	3.0	NR
24G												Sd	2	2.0	NR
24H												Sd	2	5.0	NR
25	1	4.5	0	NR	9	31.3	0	A2	0	0.0	0	D	0	0.0	D
25B												A2dor	7	18.2	A2
25C												A1dor	4	9.0	A1
25D												A1dor	4	8.0	A1
25E												Sd	2	5.0	NR
25F												A1dor	4	8.0	A1
25G												Sd	1	2.0	NR
26	12	47.5	137	A2	4	15.3	0	A2	1	3.5	0	NR	9	36.0	A2
27A	4	14.8	0	A1	1	1.3	0	NR	0	0.0	0	D	0	0.0	D
27B	1	NA	0	NR	0	0.0	0	D	0	0.0	0	D	0	0.0	D
27C								Sd	1	2.3	0	NR	2	5.0	NR
27D								Sd	1	2.0	0	NR	2	7.0	A1
27E												Sd	3	5.0	NR
27F												Sd	2	4.0	NR
27G												Sd	1	3.0	NR
27H												Sd	2	2.0	NR
27I												Sd	1	1.0	NR
28	1	3.9	0	NR	0	0.0	0	D	0	0.0	0	D	0	0.0	D
28A								A1dor	1	5.5	6	A1	0	0.0	D

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
28B									1	0.0	0	Sd	2	7.0	A1
28C												Sd	1	2.0	NR
28D												Sd	2	4.0	NR
28E												Sd	1	1.0	NR
29	2	3.7	0	NR	2	4.2	0	A1	1	1.9	0	NR	2	3.0	NR
30	3	15.5	71	A1	3	19.2	42	A2	8	38.4	8	A2	6	30.0	A2
31	3	21.9	107	A2	1	5.4	0	NR	0	0.0	0	NRdor	15	60.0	A3
32	3	8.3	11	A1	3	5.8	21	NR	2	4.3	8	NR	1	5.0	NR
33A	7	38.5	133	A2	0	0.0	0	A2dor	2	7.5	0	A1	10	56.0	A2
33B				Sd	1	5.6	0	NR	0	0.0	0	D	0	0.0	D
34	9	44.3	283	A2	14	67.5	182	A3	6	26.9	197	A2	14	58.8	A3
35	7	31.2	86	A2	3	10.4	0	A1	4	11.6	0	A2	7	26.6	A2
35B												Sd	1	2.0	NR
36	3	10.6	9	A1	0	0.0	0	A1dor	1	5.1	0	NR	8	30.4	A2
37	12	67.7	244	A3	8	41.1	109	A2	5	27.4	139	A2	5	23.0	A2
37B												A3dor	12	69.6	A3
38	8	43.0	256	A2	7	26.9	0	A2	0	0.0	0	A2dor	2	3.0	NR
39	4	17.8	74	A2	0	0.0	0	D	0	0.0	0	D	0	0.0	D
40	6	38.6	194	A2	7	35.3	0	A2	0	0.0	0	D	0	0.0	D
41A	1	4.2	0	NR	6	23.9	105	A2	7	43.1	119	A2	0	0.0	D
41B				A2dor	11	52.4	354	A2	4	17.4	2	A2	0	0.0	D
42A	1	6.5	0	A1	9	47.3	126	A2	5	38.0	185	A2	0	0.0	D
42B				A2dor	6	28.0	114	A2	9	58.3	157	A3	14	61.6	A3
42C												Sd	4	6.0	NR
43	5	32.9	180	A2	0	0.0	0	D	0	0.0	0	D	0	0.0	D
44	24	159.8	331	A3	4	13.1	0	A1	0	0.0	0	D	0	0.0	D
45	7	27.7	62	A2	6	17.6	60	A2	10	49.2	3	A2	3	11.0	A1
46	2	6.9	25	A1	2	7.8	44	A1	11	50.6	103	A2	6	24.0	A2
47	2	7.3	33	A1	4	17.2	0	A2	0	0.0	0	D	0	0.0	D
48	7	28.2	84	A2	3	9.3	0	A1	2	10.4	14	A1	1	3.0	NR
49	2	7.3	14	A1	2	6.0	24	NR	1	5.5	16	NR	2	3.0	NR
50	3	10.7	57	A1	12	52.8	305	A2	15	111.9	501	A3	16	92.8	A3

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
51	1	5.8	44	NR	2	8.7	84	A1	1	6.4	10	A1	4	13.0	A1
52	16	116.5	614	A3	16	77.1	160	A3	34	208.1	1591	A3	27	178.2	A3
53	6	30.8	137	A2	0	0.0	0	A2dor	1	1.9	0	NR	1	1.0	NR
54	5	20.9	126	A2	2	5.8	50	NR	0	0.0	0	NRdor	2	5.0	NR
55	6	34.8	241	A2	9	37.6	76	A2	15	120.0	468	A3	8	41.6	A2
55A								Sd	2	6.0	11	NR	7	21.0	A2
55B								A2dor	4	18.9	108	A2	13	72.8	A3
56	2	11.3	112	A1	0	0.0	0	D	0	0.0	0	D	0	0.0	D
56B												Sd	1	2.0	NR
56C												Sd	1	2.0	NR
56D												A1dor	2	9.0	A1
56E												A1dor	3	15.0	A1
56F												A1dor	3	7.0	A1
57	6	18.8	84	A2	1	3.3	2	NR	3	8.1	0	A1	0	0.0	D
58A	2	7.9	14	A1	3	9.6	0	A1	0	0.0	0	D	0	0.0	D
58B				A2dor	8	30.9	115	A2	15	105.6	501	A3	27	151.2	A3
58C								Sd	2	4.7	0	NR	2	6.0	NR
58D								A2dor	6	24.6	0	A2	14	78.4	A3
58E												A1dor	2	7.0	A1
59	4	15.4	57	A2	2	8.0	4	A1	0	0.0	0	A1dor	1	3.0	NR
60	2	13.1	70	A1	5	17.8	5	A2	7	42.3	213	A2	12	88.8	A3
61	7	32.1	294	A2	8	36.8	104	A2	16	98.6	410	A3	25	180.0	A3
61B												A2dor	5	17.0	A2
62	2	6.4	14	A1	1	3.8	17	NR	3	11.9	186	A1	9	48.6	A2
62B												A1dor	3	13.0	A1
63	7	43.8	237	A2	4	11.1	0	A1	8	36.2	122	A2	12	69.6	A3
64	13	55.9	148	A2	0	0.0	0	D	0	0.0	0	D	0	0.0	D
65	11	53.7	336	A2	5	23.6	49	A2	13	68.4	190	A3	16	89.6	A3
66	14	72.5	409	A3	6	26.5	60	A2	4	23.1	120	A2	6	28.8	A2
67A	18	88.9	385	A3	11	40.5	172	A2	14	84.6	700	A3	6	31.2	A2
67B												A1dor	2	8.0	A1
68	1	2.1	0	NR	0	0.0	0	NRdor	4	21.3	111	A2	6	30.0	A2

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
69	2	8.8	0	A1	0	0.0	0	D	0	0.0	0	D	0	0.0	D
69A								A2dor	4	22.0	131	A2	9	52.2	A2
70	6	19.0	210	A2	7	29.4	161	A2	14	82.6	297	A3	14	81.2	A3
71	6	18.4	18	A2	6	16.4	18	A2	4	12.5	0	A1	6	16.8	A2

Table A.2.2. Data for individual plants at the Filtration Pond site for 1995, 1996, 1997, and 1998.

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
1	19	131.1	171	A3	9	36.5	0	A2	0			A2dor	5	15.0	A1
2A	10	50.0	138	A2	8	34.2	8	A2	0			A2dor	3	3.0	A1
2B												A1dor	2	4.0	A1
3	10	51.8	30	A2	16	67.2	0	A3	0			A3dor	2	5.0	NR
4A	2	5.5	0	NR	0	0.0	0	NRdor	0			NRdor	1	2.0	NR
4B												Sd	2	5.0	NR
4C												Sd	1	2.0	NR
5	12	55.7	79	A2	8	36.6	48	A2	0			A2dor	3	5.0	NR
6	4	16.3	0	A2	0	0.0	0	A2dor	0			D	0	0.0	D
7	3	14.2	26	A1	8	36.0	40	A2	0			A2dor	1	4.0	NR
8	8	45.4	110	A2	2	7.0	0	A1	0			A1dor	0	0.0	D
9	10	45.0	76	A2	6	21.2	9	A2	0			A2dor	0	0.0	D
10	5	15.9	115	A2	5	21.4	0	A2	0			A2dor	1	2.0	NR
11	5	21.3	70	A2	12	49.4	0	A2	0			A2dor	0	0.0	D
12A	7	36.1	34	A2	5	21.4	0	A2	0			A2dor	2	6.0	NR
12B												Sd	1	1.0	NR
12C												Sd	1	3.0	NR
13	5	20.9	45	A2	12	59.8	0	A3	0			A3dor	4	6.0	NR
14	7	32.5	119	A2	13	57.5	0	A3	0			A3dor	4	8.0	A1
15A	15	61.2	42	A3	7	27.3	0	A2	0			A2dor	1	2.0	NR
15B												A1dor	3	11.0	A1
15C												Sd	1	1.0	NR
16	4	18.1	216	A2	13	47.3	26	A2	0			A2dor	5	11.0	A1
17	3	11.3	6	A1	4	12.7	0	A1	0			A1dor	2	3.0	A1
18	4	15.0	20	A1	6	13.7	0	A1	0			A1dor	3	4.0	A1
19	4	37.6	8	A2	8	22.4	44	A2	0			A2dor	10	24.0	A2
20A	1	3.9	0	NR	1	1.4	0	NR	0			NRdor	3	4.0	A1
20B												Sd	1	1.0	NR
20C												Sd	1	3.0	NR
20D												Sd	1	2.0	NR
20E												A1dor	2	3.0	A1

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
20F												Sd	1	3.0	NR
20G												Sd	1	1.0	NR
20H												Sd	1	2.0	NR
20I												Sd	1	3.0	NR
20J												Sd	1	1.0	NR
20K												Sd	1	2.0	NR
20L												Sd	1	0.0	NR
20M												Sd	1	1.0	NR
21	7	54.2	217	A2	22	118.8	30.8	A3	0			A3dor	0	0.0	D
22A	4	26.4	84	A2	7	34.6	42	A2	0			A2dor	1	5.0	NR
22B					1	0.0	0	Sd	0			Sd	1	3.0	NR
23	5	17.1	19	A2	11	51.7	77	A2	0			A2dor	0	0.0	D
24	2	8.8	24	A1	3	15.5	0	A2	0			A2dor	1	3.0	NR
25A	6	44.0	52	A2	6	35.9	6	A2	0			A2dor	4	10.0	A1
25B												Sd	1	2.0	NR
25C												Sd	1	1.0	NR
25D												Sd	1	2.0	NR
25E												Sd	1	2.0	NR
26A	14	122.1	487	A3	24	127.7	139.2	A3	0			A3dor	0	0.0	D
26B				A2dor	6	16.9	24	A2	0			A2dor	0	0.0	D
27	4	26.5	35	A2	9	42.7	18	A2	0			A2dor	0	0.0	D
28	14	64.7	0	A3	14	53.2	14	A2	0			A2dor	0	0.0	D
29	7	48.2	166	A2	16	112.3	198.4	A3	0			A3dor	0	0.0	D
30	19	98.4	152	A3	14	63.3	23.333	A3	0			A3dor	0	0.0	D
31	5	26.8	0	A2	5	18.6	18.333	A2	0			A2dor	0	0.0	D
32	1	6.9	3	A1	5	20.0	0	A2	0			A2dor	0	0.0	D
33	3	22.8	59	A2	5	17.7	20	A2	0			A2dor	0	0.0	D
34	17	116.3	210	A3	12	47.5	0	A2	0			A2dor	0	0.0	D
35	20	126.0	80	A3	39	203.6	187.2	A3	0			A3dor	0	0.0	D
36	10	79.2	280	A3	20	133.6	36	A3	0			A3dor	0	0.0	D
37	50	345.0	590	A3	51	348.8	377.4	A3	0			A3dor	0	0.0	D
38	11	68.4	125	A3	16	80.3	32	A3	0			A3dor	0	0.0	D

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
39	12	64.3	65	A3	14	73.1	78.4	A3	0			A3dor	0	0.0	D
40	16	87.7	128	A3	21	92.4	134.4	A3	0			A3dor	0	0.0	D
41	30	230.4	600	A3	53	358.3	307.4	A3	0			A3dor	0	0.0	D
42A	1	3.9	5	NR	4	16.3	66	A2	0			A2dor	0	0.0	D
42B												Sd	1	1.0	NR
42C												A1dor	5	9.0	A1
43	9	40.9	9	A2	10	39.2	40	A2	0			A2dor	0	0.0	D
44	3	9.9	0	A1	1	5.1	0	NR	0			NRdor	0	0.0	D
45	9	41.4	90	A2	5	17.8	0	A2	0			A2dor	0	0.0	D
46	10	51.6	83	A2	22	106.5	0	A3	0			A3dor	0	0.0	D
47	16	115.2	93	A3	30	193.2	288	A3	0			A3dor	0	0.0	D
48	12	80.9	12	A3	17	98.3	68	A3	0			A3dor	0	0.0	D
49	29	247.7	481	A3	54	369.4	129.6	A3	0			A3dor	0	0.0	D
50A	10	71.6	33	A3	20	106.0	12	A3	0			A3dor	1	1.0	NR
50B												Sd	2	6.0	NR
50C												Sd	1	1.0	NR
50D												Sd	1	2.0	NR
51A	22	166.3	220	A3	30	201.0	30	A3	0			A3dor	4	15.0	A1
51B												A1dor	3	8.0	A1
52	14	84.6	123	A3	25	159.0	30	A3	0			A3dor	0	0.0	D
53A	5	14.8	5	A1	15	84.6	12	A3	0			A3dor	0	0.0	D
53B												Sd	1	3.0	NR
53C												Sd	1	1.0	NR
54	2	2.2	0	A1	6	20.5	12	A2	0			A2dor	1	4.0	NR
55	4	5.7	0	NR	9	62.5	0	A3	0			A3dor	5	19.0	A2
56	5	11.6	0	A1	20	94.0	6.6667	A3	0			A3dor	8	32.0	A2
57				Sd	1	4.0	2	NR	0			NRdor	0	0.0	D
57A					1	0.0	0	Sd	0			D	0	0.0	D
58				A3dor	15	71.4	90	A3	0			A3dor	0	0.0	D

Table A.2.3. Data for individual plants at the Frozen Head site for 1995, 1996, 1997, and 1998.

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
1	29	270.9	209	A3	25	221.5	0	A3	32	268.2	64	A3	3	21.0	A2
2	4	31.4	82	A2	2	21.0	34	A2	5	35.8	20	A2	2	6.0	A1
3	7	85.5	295	A3	6	49.3	57	A2	14	109.5	126	A3	12	79.2	A3
4	6	64.0	155	A3	20	183.2	200	A3	16	124.5	35	A3	5	20.0	A2
5	31	301.9	533	A3	26	265.2	338	A3	31	247.4	93	A3	0	0.0	A3dor
6	17	156.7	187	A3	6	45.0	0	A2	9	60.8	31	A3	14	72.8	A3
7	20	129.6	24	A3	4	23.5	0	A2	4	25.5	0	A2	6	28.8	A2
8	21	243.2	256	A3	9	61.0	72	A3	10	85.6	50	A3	12	96.0	A3
9	40	443.2	112	A3	22	202.4	97	A3	32	320.6	96	A3	1	8.0	A1
9A	2	12.1	2	A1	3	16.6	12	A2	1	6.0	0	NR	4	14.0	A1
9B				A1dor	2	13.1	0	A1	3	22.9	0	A2	3	13.0	A1
9C								A1dor	2	8.3	0	A1	2	9.0	A1
10A				A1dor	3	14.4	0	A1	2	10.6	2	A1	4	15.0	A1
10B	13	134.7	62	A3	14	92.7	3	A3	13	101.9	5	A3	0	0.0	A3dor
11	17	152.7	31	A3	4	27.5	4	A2	4	26.2	38	A2	6	27.6	A2
12	20	174.0	184	A3	17	126.5	0	A3	17	145.9	235	A3	12	96.0	A3
13A	7	43.3	12	A2	7	39.3	0	A2	6	43.1	22	A2	3	17.0	A2
13B								A2dor	6	43.7	14	A2	0	0.0	A2dor
13C								A1dor	1	6.2	0	A1	2	15.0	A1
14	9	67.7	43	A3	7	46.8	5	A2	9	59.6	38	A3	7	42.0	A2
15	20	170.8	132	A3	21	173.9	176	A3	35	296.1	539	A3	25	180.0	A3
16	9	71.8	108	A3	12	93.8	115	A3	17	148.6	201	A3	8	36.8	A2
16B												A1dor	3	10.0	A1
17A	4	24.6	32	A2	7	62.2	4	A3	4	31.0	12	A2	12	108.0	A3
17B								A1dor	1	6.2	0	A1	3	11.0	A1
17C								A1dor	3	12.1	9	A1	6	25.2	A2
18	5	36.7	101	A2	5	37.4	4	A2	5	40.6	45	A2	0	0.0	A2dor
19A	17	160.5	462	A3	21	150.4	273	A3	16	124.2	115	A3	17	102.0	A3
19B								A1dor	3	14.5	0	A1	4	22.0	A2
19C												Sd	1	3.0	NR
20	7	35.4	31	A2	10	52.0	3	A2	7	42.1	35	A2	7	32.2	A2

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
21	2	8.9	0	A1	7	35.6	32	A2	10	67.6	12	A3	17	91.8	A3
22	7	42.1	48	A2	7	35.8	28	A2	1	8.5	0	A1	0	0.0	A1dor
23	2	15.6	33	A2	9	58.3	7	A3	10	99.2	118	A3	8	54.4	A2
24	1	5.5	13	NR	11	112.4	339	A3	27	301.9	513	A3	3	18.0	A2
25A				Sd	1	3.2	0	NR	2	12.2	14	A1	0	0.0	A1dor
25B				Sd	1	3.7	0	NR	1	6.3	4	A1	3	22.0	A2
25C				Sd	1	2.6	0	NR	3	19.3	21	A2	4	18.0	A2
25D				Sd	1	2.6	0	NR	4	19.6	14	A2	6	30.0	A2
25E				Sd	1	2.5	0	NR	5	20.3	7	A2	8	44.8	A2
25F				Sd	1	1.4	0	NR	2	10.5	2	A1	4	30.0	A2
25G				Sd	1	1.4	0	NR	2	10.5	22	A1	5	27.0	A2
25H				A1dor	2	7.4	0	A1	4	26.8	35	A2	2	10.0	A1
25I				Sd	1	1.3	0	NR	2	8.9	2	A1	4	25.0	A2
25J	19	202.2	1132	A3	18	163.8	688	A3	13	126.1	419	A3	1	3.0	NR
25K												Sd	2	6.0	NR
25L												Sd	1	3.0	NR
26	6	57.7	412	A3	14	144.5	344	A3	13	107.6	192	A3	13	109.2	A3
26A	1	5.3	8	NR	4	22.7	25	A2	2	15.5	26	A2	1	5.0	NR
27	1	9.1	37	A1	4	40.5	97	A2	5	44.0	50	A2	4	19.0	A2
27B												Sd	1	3.0	NR
27C												Sd	1	3.0	NR
28	11	80.1	128	A3	20	126.8	320	A3	7	41.7	91	A2	0	0.0	D
29	18	150.8	191	A3	29	217.5	87	A3	12	46.3	0	A2	14	98.0	A3
30	11	77.9	0	A3	12	81.6	168	A3	0	0.0	0	A3dor	0	0.0	D
31A				Sd	1	2.2	0	NR	1	5.0	3	NR	4	19.0	A2
31B	10	81.2	278	A3	13	98.0	10	A3	8	57.4	59	A3	12	84.0	A3
32	3	15.8	0	A2	9	65.9	27	A3	14	98.3	17	A3	12	79.2	A3
33	7	39.9	21	A2	9	55.8	5	A2	1	4.9	2	NR	1	7.0	A1
34	18	123.5	0	A3	10	50.8	0	A2	10	53.2	4	A2	12	72.0	A3
35	1	1.7	0	NR	2	10.5	0	A1	4	24.4	0	A2	7	35.0	A2
36	4	21.6	100	A2	5	29.3	0	A2	1	5.0	1	NR	4	19.0	A2
37	8	33.4	0	A2	6	34.9	0	A2	2	17.6	0	A1	9	55.8	A2

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
38	9	58.5	18	A3	9	53.5	0	A2	10	49.4	0	A2	15	84.0	A3
39	15	69.0	0	A3	3	8.1	0	A1	1	2.6	0	NR	1	3.0	NR
40	3	10.7	0	A1	4	8.8	0	A1	1	3.2	0	NR	0	0.0	NRdor
41A				Sd	1	2.2	0	NR	2	8.1	0	A1	3	9.0	A1
41B	3	7.5	0	A1	1	1.8	0	NR	0	0.0	0	NRdor	0	0.0	D
42	3	20.9	11	A2	2	9.8	0	A1	2	8.4	0	A1	2	7.0	A1
43	3	13.4	2	A1	7	29.3	0	A2	6	34.7	18	A2	9	46.8	A2
44	7	34.7	0	A2	7	23.8	0	A2	6	25.0	0	A2	6	21.6	A2
45A				Sd	1	3.3	0	NR	2	6.5	0	A1	3	8.0	A1
45B	1	2.7	0	NR	1	4.7	0	NR	0	0.0	0	NRdor	2	6.0	NR
46	3	10.7	0	A1	0	0.0	0	A1dor	0	0.0	0	D	0	0.0	D
47	4	16.9	0	A2	0	0.0	0	A2dor	0	0.0	0	D	0	0.0	D
48	4	16.0	0	A2	1	2.5	0	NR	0	0.0	0	NRdor	0	0.0	D
48A				Sd	1	3.5	0	NR	2	4.1	0	NR	2	5.0	NR
48B				Sd	1	NA	0	NR	0	0.0	0	NRdor	0	0.0	D
48C				Sd	1	5.2	0	NR	0	0.0	0	NRdor	0	0.0	D
48D				A1dor	2	8.3	0	A1	0	0.0	0	A1dor	0	0.0	D
48E				A1dor	4	11.0	0	A1	0	0.0	0	A1dor	0	0.0	D
48F				Sd	1	4.7	0	NR	0	0.0	0	NRdor	0	0.0	D
49	11	50.2	11	A2	5	23.0	0	A1	1	3.8	0	NR	1	3.0	NR
50A	7	37.0	5	A2	1	3.0	0	NR	1	2.8	0	NR	0	0.0	NRdor
50B								Sd	1	2.4	0	NR	1	3.0	NR
51	8	33.1	0	A2	3	10.8	0	A1	1	3.2	0	NR	1	4.0	NR

Table A.2.4. Data for individual plants at the Grassy Creek site for 1995, 1996, 1997, and 1998.

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
1	10	60.4	306	A3	12	62.4	312	A3	8	54.6	34	A2	0	0.0	A2dor
2A	2	NA	0	A1	1	6.1	9	A1	4	27.0	0	A2	0	0.0	A2dor
2AA								Sd	1	NA	0	NR	1	6.0	NR
2AB								Sd	1	NA	0	NR	0	0.0	NRdor
2B	2	10.0	0	A1	5	11.6	0	A1	0	0.0	0	A1dor	0	0.0	D
2C	3	NA	0	A1	1	4.7	0	NR	2	13.9	0	A1	3	16.0	A2
2D								Sd	1	3.5	3	NR	2	6.0	A1
2E								Sd	1	2.3	0	NR	1	3.0	NR
2F								Sd	1	1.4	0	NR	1	2.0	NR
2G								Sd	1	2.4	0	NR	3	11.0	A1
2H								Sd	1	1.5	0	NR	0	0.0	NRdor
2I								Sd	1	2.9	2	NR	2	10.0	A1
2J								Sd	1	3.0	0	NR	1	4.0	NR
2K								Sd	1	2.3	0	NR	1	5.0	NR
2L								Sd	1	1.9	0	NR	0	0.0	NRdor
2M								Sd	1	1.8	0	NR	0	0.0	NRdor
2N								Sd	1	2.6	0	NR	1	3.0	NR
2P								Sd	1	1.7	0	NR	0	0.0	NRdor
2Q								Sd	1	1.1	0	NR	0	0.0	NRdor
2R								Sd	1	1.1	0	NR	0	0.0	NRdor
2S								Sd	1	2.3	0	NR	0	0.0	NRdor
2T								Sd	1	1.2	0	NR	0	0.0	NRdor
2U								Sd	1	3.1	2	NR	0	0.0	NRdor
2V								Sd	2	3.0	0	NR	0	0.0	NRdor
2W								Sd	2	2.1	0	NR	0	0.0	NRdor
2X								Sd	1	2.3	0	NR	0	0.0	NRdor
2Y								Sd	1	2.0	0	NR	0	0.0	NRdor
2Z								Sd	1	2.2	0	NR	0	0.0	NRdor
3A	2	NA	0	A1	1	2.3	2	NR	0	0.0	0	NRdor	0	0.0	D
3B	4	10.0	0	A1	1	3	5	NR	0	0.0	0	NRdor	0	0.0	D
4	6	29.3	0	A2	3	14.1	0	A1	0	0.0	0	A1dor	0	0.0	D

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
5A	2	5.3	0	NR	0	0.0	0	NRdor	0	0.0	0	D	0	0.0	D
5B	4	NA	0	A1	1	3.1	0	NR	0	0.0	0	NRdor	0	0.0	D
5C								Sd	1	2.8	0	NR	0	0.0	NRdor
5D								Sd	1	4.4	0	NR	0	0.0	NRdor
5E								Sd	2	2.3	0	NR	1	6.0	NR
5F								A1dor	4	13.7	8	A1	0	0.0	A1dor
6A	3	NA	0	A1	4	18.7	0	A2	4	17.5	0	A2	2	4.0	NR
6B	3	13.4	0	A1	4	8.4	0	A1	1	2.0	0	NR	0	0.0	NRdor
6C								Sd	1	3.3	0	NR	3	14.0	A1
6D								Sd	1	1.4	0	NR	0	0.0	NRdor
6E								Sd	1	1.3	0	NR	0	0.0	NRdor
6F								Sd	1	1.5	0	NR	1	6.0	NR
7	3	16.5	79	A2	4	20.9	67	A2	4	17.4	0	A2	0	0.0	A2dor
8	1	6.9	28	A1	6	31.0	156	A2	4	22.8	0	A2	2	4.0	NR
9	6	29.0	150	A2	12	50.6	60	A2	13	62.7	0	A3	2	3.0	NR
10	2	9.8	16	A1	6	20.6	5	A2	2	12.2	0	A1	1	2.0	NR
10B								Sd	1	1.1	0	NR	1	2.0	NR
10C								Sd	1	2.2	0	NR	2	7.0	A1
11	6	39.4	170	A2	6	36.4	26	A2	11	77.7	0	A3	11	52.8	A2
12	3	12.2	65	A1	0	0.0	0	A1dor	0	0.0	0	D	0	0.0	D
13	1	5.2	21	A1	2	10.6	26	A1	1	5.0	0	NR	7	11.2	A1
14	3	8.1	2	A1	0	0.0	0	A1dor	0	0.0	0	D	0	0.0	D
14B								Sd	1	1.9	0	NR	2	6.0	NR
15	6	36.5	126	A2	6	29.4	52	A2	7	38.6	0	A2	0	0.0	A2dor
16	2	9.3	30	A1	4	17.5	16	A2	4	22.9	0	A2	8	19.2	A2
16B				Sd	2	5.2	0	NR	2	5.3	0	NR	5	13.0	A1
17	4	17.2	0	A2	5	16.6	0	A2	10	88.0	50	A3	4	13.0	A1
17B								Sd	1	1.4	0	NR	0	0.0	NRdor
17C								Sd	1	1.1	0	NR	0	0.0	NRdor
18A	8	47.0	123	A2	9	48.2	95	A2	10	66.2	0	A3	2	4.0	NR
18B					1	0.0	0	Sd	2	4.7	0	NR	0	0.0	NRdor
18C								Sd	1	1.5	0	NR	0	0.0	NRdor

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
18D								Sd	1	4.9	0	NR	0	0.0	NRdor
19A	1	4.7	12	NR	2	13.8	85	A1	8	67.5	0	A3	0	0.0	A3dor
19B					1	0.0	0	Sd	1	2.5	0	NR	0	0.0	NRdor
19C					1	0.0	0	Sd	0	0.0	0	D	0	0.0	D
19D								Sd	1	4.4	0	NR	0	0.0	NRdor
19E								Sd	2	6.1	0	A1	0	0.0	A1dor
19F								Sd	1	2.7	0	NR	0	0.0	NRdor
19G								Sd	1	2.0	0	NR	0	0.0	NRdor
19H								Sd	1	2.7	0	NR	0	0.0	NRdor
19I								Sd	1	2.1	0	NR	0	0.0	NRdor
19J								Sd	1	2.0	0	NR	0	0.0	NRdor
20A	1	3.2	0	NR	0	0.0	0	NRdor	0	0.0	0	D	0	0.0	D
20B	3	NA	0	NR	3	10.7	0	A1	4	25.2	0	A2	0	0.0	A2dor
20C	1	NA	0	NR	1	2.1	0	NR	1	7.5	0	A1	1	2.0	NR
20D	1	NA	0	NR	1	0.9	0	NR	0	0.0	0	NRdor	0	0.0	D
21A	1	NA	0	NR	1	2.4	0	NR	1	5.3	0	NR	0	0.0	NRdor
21B	1	0.0	0	Sd	1	0.0	0	Sd	0	0.0	0	D	0	0.0	D
21C	1	5.8	0	NR	2	7.3	0	A1	7	44.0	96	A2	1	7.0	A1
21D	1	0.0	0	Sd	1	0.0	0	Sd	0	0.0	0	D	0	0.0	D
21E								Sd	1	0.9	0	NR	1	3.0	NR
21F								Sd	1	2.3	0	NR	1	4.0	NR
21G								Sd	1	1.5	0	NR	1	6.0	NR
21H								Sd	1	1.1	0	NR	1	4.0	NR
21I								Sd	1	1.5	0	NR	0	0.0	NRdor
21J								Sd	1	1.2	0	NR	0	0.0	NRdor
21K								Sd	1	3.6	4	NR	1	5.0	NR
22	7	32.6	28	A2	9	34.9	36	A2	12	76.3	334	A3	7	33.6	A2
23	1	3.2	0	NR	2	7.0	14	A1	4	30.7	0	A2	2	16.0	A2
24	2	2.0	0	NR	1	1.4	0	NR	2	2.8	0	NR	1	3.5	NR
25	2	3.8	0	NR	3	10.1	12	A1	5	27.4	0	A2	4	25.0	A2
26	3	3.9	0	NR	4	22.7	88	A2	6	38.0	104	A2	5	29.0	A2
27	2	9.3	0	A1	2	5.4	4	NR	3	11.7	5	A1	1	7.0	A1

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
28	2	10.2	0	A1	4	16.5	30	A2	2	13.5	0	A1	3	12.0	A1
29	4	17.1	0	A2	8	47.0	48	A2	4	22.1	0	A2	5	22.0	A2
30	1	4.4	0	NR	3	16.5	22	A2	6	34.4	0	A2	7	39.2	A2
31	2	6.8	0	A1	3	12.1	20	A1	8	36.5	48	A2	4	19.0	A2
32A	2	8.0	0	A1	4	20.0	32	A2	9	63.2	104	A3	3	14.0	A1
32B	1	NA	0	NR	1	1.0	0	NR	1	1.5	0	NR	1	3.0	NR
33	2	8.4	0	A1	1	3.8	0	NR	1	5.2	0	NR	1	5.0	NR
34	4	16.4	0	A2	3	13.3	4	A1	3	14.8	0	A1	2	12.0	A1
35	6	24.2	4	A2	10	61.8	80	A3	12	104.9	22	A3	5	23.0	A2
36A	1	2.6	0	NR	2	5.7	4	NR	4	28.0	0	A2	4	18.0	A2
36B	2	NA	0	A1	3	9.0	5	A1	3	24.2	56	A2	3	15.0	A1
36C								Sd	1	1.6	0	NR	1	6.0	NR
36D								Sd	1	1.3	0	NR	0	0.0	NRdor
37	2	11.4	0	A1	3	9.4	0	A1	9	40.3	2	A2	9	52.2	A2
38A	1	2.8	16	NR	2	8.9	28	A1	4	24.7	0	A2	0	0.0	A2dor
38B	3	NA	0	NR	2	4.5	16	NR	3	9.0	3	A1	0	0.0	A1dor
39	2	6.4	0	A1	5	14.9	49	A1	9	37.6	14	A2	6	14.4	A1
40	2	4.8	1	NR	3	9.4	0	A1	3	12.9	0	A1	3	12.0	A1
41A	1	2.9	0	NR	2	4.7	0	NR	2	11.8	0	A1	0	0.0	A1dor
41B	1	NA	0	NR	1	1.1	0	NR	1	2.2	0	NR	1	3.0	NR
41C								Sd	1	2.1	0	NR	2	12.0	A1
41D								Sd	1	0.8	0	NR	1	1.0	NR
41E								Sd	1	2.0	0	NR	1	3.0	NR
41F								Sd	1	1.3	0	NR	2	3.0	NR
41G								Sd	2	2.7	0	NR	3	7.0	A1
41H								Sd	1	1.1	0	NR	1	1.5	NR
42	1	2.3	0	NR	1	1.1	0	NR	0	0.0	0	NRdor	0	0.0	D
43	2	6.0	0	NR	4	16.2	11	A2	9	63.5	59	A3	6	27.6	A2
44	1	3.0	0	NR	1	4.7	0	NR	3	12.1	19	A1	4	17.0	A2
44B								Sd	1	2.8	0	NR	1	4.0	NR
45	3	10.6	2	A1	0	0.0	0	A1dor	0	0.0	0	D	0	0.0	D
46	4	21.4	60	A2	4	16.9	31	A2	4	27.2	122	A2	5	24.0	A2

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
46B								A1dor	2	6.8	1	A1	0	0.0	A1dor
47	1	6.4	23	A1	3	9.5	30	A1	5	22.3	205	A2	0	0.0	A2dor
48	3	18.1	0	A2	5	16.1	0	A2	5	23.6	54	A2	4	17.0	A2
48B								Sd	1	1.2	0	NR	0	0.0	NRdor
49	4	21.9	0	A2	2	7.4	0	A1	2	3.7	0	NR	0	0.0	NRdor
50A	1	1.9	0	NR	1	2.6	0	NR	1	5.2	0	NR	1	6.0	A1
50B					1	3.0	0	NR	3	12.1	24	A1	3	16.0	A2
50C					1	1.8	0	NR	4	17.1	39	A2	4	16.0	A2
50D								Sd	1	0.9	0	NR	1	3.0	NR
50E								Sd	1	2.6	0	NR	3	13.0	A1
50F								Sd	1	3.4	0	NR	5	27.0	A2
50G								Sd	1	1.0	0	NR	1	1.0	NR
51	3	6.9	0	A1	1	3.3	5	NR	1	3.0	0	NR	1	4.0	NR
52	7	24.5	0	A2	4	16.9	7	A2	10	43.8	152	A2	4	10.0	A1
53	4	13.5	0	A1	5	16.4	3	A2	6	26.0	57	A2	6	28.8	A2
54	8	41.8	0	A2	7	34.6	42	A2	10	82.0	170	A3	3	14.0	A1
55	3	16.2	144	A2	2	12.5	0	A1	7	45.4	98	A2	3	19.0	A2
56	3	NA	0	NR	3	10.4	0	A1	4	25.5	116	A2	2	18.0	A2
57	4	NA	0	A1	4	12.4	19	A1	6	31.0	31	A2	3	18.0	A2
58	1	NA	0	NR	3	6.0	0	NR	3	17.1	18	A2	2	10.0	A1
817												Sd	1	1.0	NR
818												Sd	1	1.0	NR
819												Sd	1	2.0	NR
820												Sd	1	1.0	NR
821												Sd	1	2.0	NR
822												Sd	1	1.0	NR
823												Sd	1	1.0	NR
824												Sd	2	5.0	NR
825												Sd	1	1.0	NR
826												Sd	1	1.0	NR
827												Sd	1	1.0	NR
828												Sd	1	1.0	NR

Plant ID	Stem95	Area95	Fruits95	Stage95	Stem96	Area96	Fruits96	Stage96	Stem97	Area97	Fruits97	Stage97	Stem98	Area98	Stage98
829												Sd	1	1.0	NR
830												Sd	1	1.0	NR
831												Sd	1	2.0	NR
832												Sd	1	1.0	NR
833												Sd	1	3.0	NR
834												Sd	2	2.0	NR
835												Sd	1	1.0	NR
836												Sd	1	3.0	NR
837												Sd	2	2.0	NR
838												Sd	1	2.0	NR
839												Sd	1	1.0	NR
840												Sd	1	1.0	NR
841												Sd	1	1.0	NR
842												Sd	1	2.0	NR
843												Sd	1	1.0	NR
844												Sd	1	1.0	NR

Appendix 3. Analysis of Seeds per Fruit by Site and Year

Statistical analysis of data on number of seeds per fruit includes data only for those fruits without evidence of insect damage.

a. ANOVA was performed on square root transformations of the seeds-per-fruit count data; factorial design (4 sites, 3 years, and site by year interaction). (Table A.3.1). The interaction between site and year was not statistically significant ($P = 0.107$) (Fig. A.3.1).

b. The four sites differed significantly ($P = 0.021$). For CR, FP, FZ, and GC, respectively, the means were 80, 67, 64, and 71 seeds per fruit; the medians were 79, 68, 55, and 75 seeds per fruit. Based on *post hoc* tests, seeds per fruit was significantly greater at the CR site than at the FP or FZ site ($P < 0.05$), but not greater than at the GC site.

c. The differences between the three years (1995, 1996, and 1997) for which counts of seed per fruit were made were not statistically different ($P = 0.107$). In chronological order, the means were 66, 71, and 80 seeds per fruit; the medians were 68, 68, and 75 seeds per fruit.

I do not have data on seeds per fruit for each of the three reproductive stages separately for any year at any site. Given that I estimate $Sd(t)$ from $NR(t+1)$ for each site by year, site and annual differences in relative reproductive output are implicitly represented in my estimates of the three fecundity elements of the 12 site-by-year transition matrices.

Table A3.1 ANOVA for the effects of site (population) and year on number of seeds per fruit at the four sites for demographic monitoring of *A. patula* in 1995, 1996, and 1997.

Source	Sum of squares	df	Mean square	F	Signif.
Site	33.270	3	11.090	3.318	0.021
Year	15.142	2	7.571	2.265	0.107
Site X Year	30.769	5	6.154	1.841	0.107
Error	611.647	183	3.342		
Total	701.482	193			

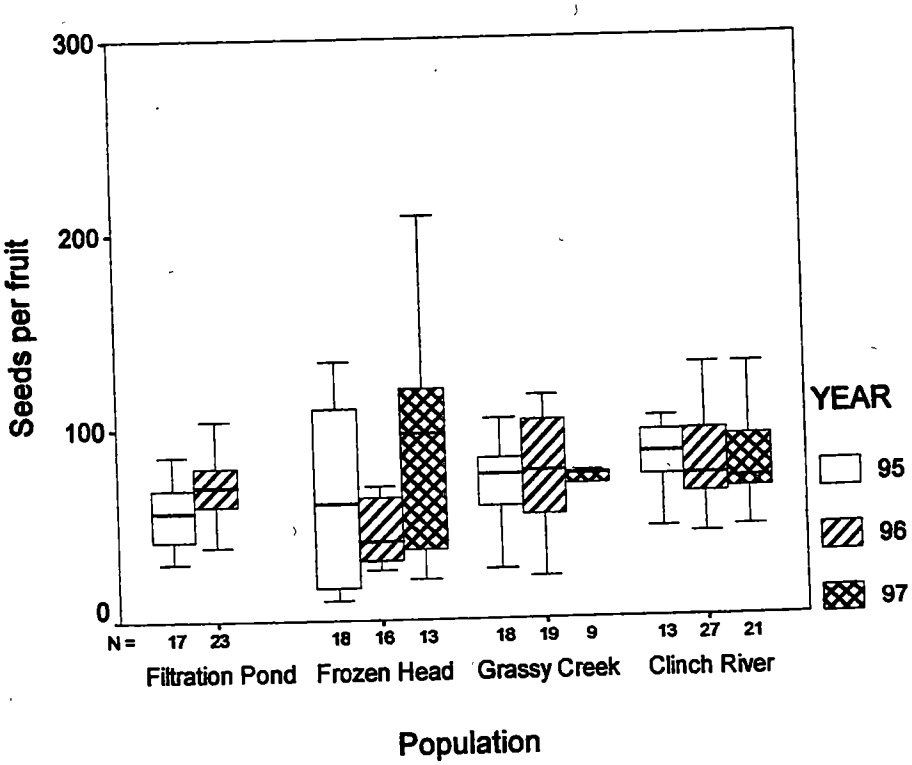


Fig. A3.1 Number of seeds per fruit as a function of site (population) and year. ANOVA results in Table A2.1. Bar in box is the median. N = number of fruits.

Appendix 4. Results of Eigenanalysis for Each Site and Transition Year

The following 12 pages are a summary of the eigenanalysis output from RAMAS Metapop (Akcakaya 1998) for each of the four sites and three transition years. Each page includes the following information in the order listed:

Stage transition matrix input to the model (9 X 9)

Population growth rate, lambda: λ

Initial stage distribution input to the model (Initial)

Projected stable stage distribution (Stable)

Stage-specific reproductive values (RV)

Ave residence time in each stage (years)

Total number of plants (N) in the initial population

Elasticity matrix (9 X 9)

Summation of elasticities for fecundity (F), growth (G), survival (S), regression (R), dormancy (D), and S+ = S + R + D

Sensitivity matrix (9 X 9)

Table A4.1 Eigenanalysis for CR 95-96

Stage matrix (CR 95-96):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.050	0	0.310	0	3.320
2: NRdor	0	0	0.400	0	0	0	0	0	0
3: NR	0.250	0	0.200	0	0.220	0	0.110	0	0
4: A1dor	0	0	0	0	0.170	0	0	0	0
5: A1	0	0	0.270	1.000	0.220	0	0.180	0	0.110
6: A2dor	0	0	0	0	0	0	0.210	0	0
7: A2	0	0	0.130	0	0.350	1.000	0.430	0	0.440
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0.040	0	0.070	1.000	0.440

Lambda, λ 1.0169 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.160	0.301	1.00	1.54
2: NRdor	0.000	0.063	0.00	1.00
3: NR	0.150	0.161	2.67	1.25
4: A1dor	0.050	0.023	5.05	1.00
5: A1	0.230	0.140	5.13	1.28
6: A2dor	0.030	0.047	6.01	1.00
7: A2	0.280	0.227	6.11	1.75
8: A3dor	0.010	0.000	11.20	1.00
9: A3	0.090	0.037	11.39	1.79
Total N	100			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.028	0	0	0	*0.002*	0	0.019	0	0.033
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.054	0	0.023	0	0.022	0	0.018	0	0
4: A1dor	0	0	0	0	0.032	0	0	0	0
5: A1	0	0	0.060	0.032	0.043	0	0.056	0	*0.006*
6: A2dor	0	0	0	0	0	0	**0.077**	0	0
7: A2	0	0	0.034	0	**0.081**	0.077	**0.160**	0	0.027
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	*0.017*	0	0.049	0	0.050
Sum	0.082	0.000	0.117	0.032	0.197	0.077	0.379	0.000	0.116
F=	0.054	G=	0.294	S=	0.413	R=	0.129	D=	0.109
				S+=	0.652				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.082	0.017	0.044	*0.006*	0.038	0.013	0.062	0	*0.010*
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.220	0.046	0.117	*0.017*	0.102	0.034	0.165	0	0.027
4: A1dor	0.415	0.087	0.221	0.032	0.193	0.065	0.313	0	0.051
5: A1	0.422	0.089	0.225	0.033	0.197	0.066	0.318	0	0.052
6: A2dor	0.495	0.104	0.264	0.038	0.230	0.077	0.373	0	0.061
7: A2	0.503	0.106	0.268	0.039	0.234	0.078	0.379	0	0.062
8: A3dor	**0.922**	0.193	0.492	0.072	0.429	0.144	0.695	0	0.114
9: A3	**0.938**	0.197	0.500	0.073	0.436	0.146	**0.706**	0	0.116

Table A4.2 Eigenanalysis for CR 96-97

Stage matrix (CR 96-97):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.161	0	0.639	0	16.782
2: NRdor	0	0	0.733	0	0	0	0	0	0
3: NR	0.250	0.167	0.133	0.143	0.250	0.111	0.034	0	0.125
4: A1dor	0	0	0	0	0.400	0	0	0	0
5: A1	0	0	0.133	0.429	0.150	0.111	0.069	0	0
6: A2dor	0	0	0	0	0	0	0.207	0	0
7: A2	0	0.167	0	0	0.200	0.333	0.379	0	0.250
8: A3dor	0	0	0	0	0	0	0	0	0.125
9: A3	0	0	0	0	0	0	0.310	0	0.500

Growth rate (lambda)= 1.1204 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.299	0.570	1.00	1.54
2: NRdor	0.045	0.118	3.12	1.00
3: NR	0.112	0.181	3.08	1.15
4: A1dor	0.052	0.012	2.57	1.00
5: A1	0.149	0.035	5.70	1.18
6: A2dor	0.067	0.009	6.17	1.00
7: A2	0.216	0.048	17.83	1.61
8: A3dor	0.000	0.003	0.00	1.00
9: A3	0.060	0.024	34.86	2.00
Total N	134			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.051	0	0	0	*0.001*	0	0.008	0	0.104
2: NRdor	0	0	0.106	0	0	0	0	0	0
3: NR	**0.113**	0.016	0.019	*0.001*	0.007	*0.001*	*0.001*	0	0.002
4: A1dor	0	0	0	0	0.009	0	0	0	0
5: A1	0	0	0.035	0.008	0.008	*0.001*	0.005	0	0
6: A2dor	0	0	0	0	0	0	0.016	0	0
7: A2	0	0.090	0	0	0.032	0.014	0.084	0	0.028
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	**0.134**	0	**0.108**
Sum	0.164	0.106	0.160	0.009	0.057	0.016	0.247	0.000	0.241
F=	0.113	G=	0.404	S=	0.306	R=	0.047	D=	0.131
				S+=	0.484				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.164	0.034	0.052	0.004	0.010	0.003	0.014	*0.001*	0.007
2: NRdor	0.512	0.106	0.162	0.011	0.031	0.008	0.043	*0.002*	0.022
3: NR	0.506	0.105	0.160	0.011	0.031	0.008	0.043	*0.002*	0.021
4: A1dor	0.423	0.088	0.134	0.009	0.026	0.007	0.036	*0.002*	0.018
5: A1	0.935	0.194	0.296	0.020	0.057	0.015	0.079	0.004	0.039
6: A2dor	1.013	0.210	0.321	0.022	0.062	0.016	0.085	0.005	0.043
7: A2	**2.927**	0.607	0.927	0.064	0.178	0.046	0.247	0.014	0.123
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	**5.722**	1.186	**1.813**	0.124	0.348	0.089	0.483	0.027	0.241

Table A4.3 Eigenanalysis for CR 97-98

Stage matrix (CR 97-98):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.110	0	0.480	0	10.050
2: NRdor	0	0	0.090	0	0	0	0	0	0
3: NR	0.250	0.360	0.640	0.050	0.360	0.220	0	0	0
4: A1dor	0	0	0	0	0.180	0	0	0	0
5: A1	0.020	0	0.090	0.650	0.180	0.110	0.090	0	0
6: A2dor	0	0	0	0	0	0	0.190	0	0
7: A2	0	0	0.180	0	0.270	0.330	0.430	0	0.231
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0.090	0	0	0	0	0.290	0.670	0.769

Lambda, λ 1.2959 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.586	0.550	1.00	1.54
2: NRdor	0.041	0.017	2.58	1.00
3: NR	0.083	0.246	3.48	2.78
4: A1dor	0.075	0.006	2.06	1.00
5: A1	0.041	0.041	3.84	1.22
6: A2dor	0.034	0.012	3.33	1.00
7: A2	0.079	0.081	9.46	1.75
8: A3dor	0.011	0	12.00	1.00
9: A3	0.049	0.047	23.22	4.33

Total N 266

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.042	0	0	0	*0.001*	0	0.009	0	0.105
2: NRdor	0	0	0.013	0	0	0	0	0	0
3: NR	0.105	0.005	**0.120**	*0.000*	0.011	0.002	0	0	0
4: A1dor	0	0	0	0	0.003	0	0	0	0
5: A1	0.009	0	0.019	0.003	0.006	*0.001*	0.006	0	0
6: A2dor	0	0	0	0	0	0	0.011	0	0
7: A2	0	0	0.092	0	0.023	0.008	0.072	0	0.023
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0.008	0	0	0	0	**0.119**	0	**0.186**
Sum	0.156	0.013	0.242	0.003	0.044	0.011	0.217	0.000	0.313
F=	0.114	G=	0.374	S=	0.442	R=	0.043	D=	0.027
				S+=	0.512				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.156	0.005	0.070	*0.002*	0.012	*0.003*	0.023	0	0.014
2: NRdor	0.402	0.013	0.180	0.004	0.030	0.009	0.059	0	0.035
3: NR	0.543	0.017	0.243	0.006	0.040	0.012	0.080	0	0.047
4: A1dor	0.322	0.010	0.144	*0.003*	0.024	0.007	0.047	0	0.028
5: A1	0.599	0.019	0.268	0.006	0.044	0.013	0.088	0	0.052
6: A2dor	0.519	0.016	0.232	0.005	0.038	0.011	0.076	0	0.045
7: A2	1.476	0.046	0.660	0.015	0.109	0.032	0.217	0	0.127
8: A3dor	**1.873**	0.058	0.837	0.019	0.139	0.041	0.276	0	0.162
9: A3	**3.623**	0.113	**1.619**	0.038	0.268	0.078	0.533	0	0.313

Table A4.4 Eigenanalysis for FP 95-96

Stage matrix (FP 95-96):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.010	0	0.020	0	0.070
2: NRdor	0	0	0.250	0	0	0	0	0	0
3: NR	0.250	0	0.250	0	0.125	0	0	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	0	0	0.250	0	0.040	0	0
6: A2dor	0	0	0	0	0	0	0.040	0	0
7: A2	0	0	0.250	0	0.375	1.000	0.640	0	0.211
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0.250	0	0.250	0	0.280	1.000	0.789

Lambda, λ 1.0109 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.065	0.065	1.00	1.54
2: NRdor	0	0.006	0	1.00
3: NR	0.065	0.024	2.64	1.33
4: A1dor	0	0	0	1.00
5: A1	0.129	0.019	3.74	1.33
6: A2dor	0.016	0.014	3.92	1.00
7: A2	0.403	0.363	3.96	2.78
8: A3dor	0.016	0.000	4.04	1.00
9: A3	0.306	0.508	4.08	4.74
Total N	62			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	***0.006***	0	0	0	***0.000***	0	***0.002***	0	***0.009***
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	***0.011***	0	***0.004***	0	***0.002***	0	0	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	0	0	***0.005***	0	***0.014***	0	0
6: A2dor	0	0	0	0	0	0	***0.015***	0	0
7: A2	0	0	***0.006***	0	***0.007***	***0.015***	***0.242***	0	***0.111***
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	***0.007***	0	***0.005***	0	***0.109***	0	***0.429***
Sum	0.017	0.000	0.017	0.000	0.019	0.015	0.382	0.000	0.550
F=	0.011	G=	0.146	S=	0.701	R=	0.127	D=	0.015
				S+=	0.843				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.017	***0.002***	0.007	0	0.005	***0.004***	0.096	0	0.135
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.046	***0.004***	0.017	0	0.013	0.010	0.255	0	0.356
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0.065	0.006	0.024	0	0.019	0.014	0.361	0	0.504
6: A2dor	0.068	0.006	0.026	0	0.020	0.015	0.378	0	0.528
7: A2	0.068	0.006	0.026	0	0.020	0.015	0.382	0	0.534
8: A3dor	0.070	0.007	0.026	0	0.021	0.015	0.389	0	0.544
9: A3	0.070	0.007	0.027	0	0.021	0.016	0.394	0	0.550

Table A4.5 Eigenanalysis for FP 96-97

Stage matrix (FP 96-97):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0	0	0.757	0	3.533
2: NRdor	0	0	1.000	0	0	0	0	0	0
3: NR	0.250	0	0	0	0	0	0	0	0
4: A1dor	0	0	0	0	1.000	0	0	0	0
5: A1	0	0	0	0	0	0	0	0	0
6: A2dor	0	0	0	0	0	0	1.000	0	0
7: A2	0	0	0	0	0	0	0	0	0
8: A3dor	0	0	0	0	0	0	0	0	1.000
9: A3	0	0	0	0	0	0	0	0	0

Lambda, λ 0.35 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.033	0.266	1.00	1.54
2: NRdor	0.016	0.544	0	1.00
3: NR	0.049	0.190	0	1.00
4: A1dor	0	0	0	1.00
5: A1	0.049	0	0	1.00
6: A2dor	0.016	0	0	1.00
7: A2	0.410	0	2.16	1.00
8: A3dor	0	0	0	1.00
9: A3	0.426	0	10.09	1.00
Total	61			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	**1.000**	0	0	0	0	0	0	0	0
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0	0	0	0	0	0	0	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	0	0	0	0	0	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0	0	0	0	0	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	0	0	0
Sum	1.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
F=	0.000	G=	0.000	S=	1.000	R=	0.000	D=	0.000
				S+=	1.000				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	1	*2.041*	*0.714*	0	0	0	0	0	0
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0	0	0	0	0	0	0	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	0	0	0	0	0	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	2.163	4.414	*1.545*	0	0	0	0	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	**10.094**	**20.602**	**7.210**	0	0	0	0	0	0

Table A4.6 Eigenanalysis for FP 97-98

Stage matrix (FP 97-98):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.004	0	0.390	0	1.803
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.250	0.250	0	0	0	0.280	0	0.154	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0.250	0	0.875	0	0.160	0	0.077	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0	0	0	0.040	0	0.077	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	0	0	0

Lambda, λ 0.35 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.632	0.583	1.00	1.54
2: NRdor	0.023	0	0.01	1.00
3: NR	0	0.417	0	1.00
4: A1dor	0.047	0	0.03	1.00
5: A1	0	0	0.01	1.00
6: A2dor	0.146	0	0.13	1.00
7: A2	0	0	1.11	1.00
8: A3dor	0.152	0	0.25	1.00
9: A3	0	0	5.15	1.00

Total N 171

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	**1.000**	0	0	0	0	0	0	0	0
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0	0	0	0	0	0	0	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	0	0	0	0	0	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0	0	0	0	0	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	0	0	0

Sum 1.000

F=	0.000	G=	0.000	S=	1.000	R=	0.000	D=	0.000
				S+=	1.000				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	1	0	0.714	0	0	0	0	0	0
2: NRdor	*0.008*	0	*0.006*	0	0	0	0	0	0
3: NR	0	0	0.000	0	0	0	0	0	0
4: A1dor	0.029	0	0.020	0	0	0	0	0	0
5: A1	0.011	0	0.008	0	0	0	0	0	0
6: A2dor	0.133	0	0.095	0	0	0	0	0	0
7: A2	**1.114**	0	0.796	0	0	0	0	0	0
8: A3dor	0.248	0	0.177	0	0	0	0	0	0
9: A3	**5.151**	0	**3.680**	0	0	0	0	0	0

Table A4.7 Eigenanalysis for FZ 95-96

Stage matrix (FZ 95-96):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.014	0	0.025	0	0.144
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.250	0	0.250	0	0.143	0	0.111	0	0
4: A1dor	0	0	0	0	0.143	0	0	0	0
5: A1	0	0	0.250	1.000	0.143	0	0.167	0	0.042
6: A2dor	0	0	0	0	0	0	0.056	0	0
7: A2	0	0	0.250	0	0.571	0	0.500	0	0.292
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0.250	0	0	0	0.167	0	0.667

Lambda, λ 0.9989 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.508	0.076	1.00	1.54
2: NRdor	0	0	0	1.00
3: NR	0.034	0.107	2.60	1.33
4: A1dor	0.042	0.020	2.48	1.00
5: A1	0.059	0.140	2.48	1.17
6: A2dor	0	0.021	0	1.00
7: A2	0.153	0.370	2.42	2.00
8: A3dor	0	0	0	1.00
9: A3	0.203	0.266	2.88	3.00

Total N 118

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	*0.011*	0	0	0	*0.001*	0	*0.004*	0	0.016
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.021	0	0.029	0	0.022	0.000	0.044	0	0
4: A1dor	0	0	0	0	0.021	0	0	0	0
5: A1	0	0	0.028	0.021	0.021	0	0.064	0	0.012
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.027	0	**0.080**	0	**0.186**	0	0.078
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0.032	0	0	0	0.074	0	**0.212**
Sum	0.032	0.000	0.115	0.021	0.144	0.000	0.371	0.000	0.318
F=	0.021	G=	0.261	S=	0.479	R=	0.219	D=	0.021
				S+=	0.719				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.032	0	0.044	*0.008*	0.058	*0.009*	0.153	0	0.111
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.082	0	0.115	0.022	0.151	0.022	**0.398**	0	0.287
4: A1dor	0.079	0	0.110	0.021	0.144	0.021	**0.380**	0	0.274
5: A1	0.079	0	0.110	0.021	0.144	0.021	0.380	0	0.274
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0.077	0	0.107	*0.020*	0.140	0.021	0.371	0	0.268
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0.091	0	0.128	0.024	0.167	0.025	**0.441**	0	0.318

Table A4.8 Eigenanalysis for FZ 96-97

Stage matrix (FZ 96-97):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0	0	0.078	0	0.918
2: NRdor	0	0	0.316	0	0	0	0	0	0
3: NR	0.250	0	0.158	0	0.364	0	0.143	0	0
4: A1dor	0	0	0	0	0.182	0	0	0	0
5: A1	0	0	0.368	0.833	0.182	0	0.095	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.158	0	0.273	0.500	0.571	0	0.150
8: A3dor	0	0	0	0	0	0	0	0	0.050
9: A3	0	0	0	0	0	0	0.190	0	0.800

Lambda, λ 1.0062 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.048	0.271	1.00	1.54
2: NRdor	0	0.051	0	1.00
3: NR	0.229	0.162	2.63	1.19
4: A1dor	0.072	0.021	3.04	1.00
5: A1	0.133	0.116	3.67	1.22
6: A2dor	0.024	0	2.76	1.00
7: A2	0.253	0.193	5.55	2.33
8: A3dor	0	0.009	0	1.00
9: A3	0.241	0.177	8.49	5.00

Total N 83

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.025	0	0	0	0	0	*0.004*	0	0.043
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.047	0	0.018	0	0.029	0	0.019	0	0
4: A1dor	0	0	0	0	*0.017*	0	0	0	0
5: A1	0	0	0.058	*0.017*	0.020	0	0.018	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.038	0	0.046	0	**0.161**	0	0.039
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	**0.082**	0	**0.319**
Sum	0.072	0.000	0.113	0.017	0.113	0.000	0.284	0.000	0.401
F=	0.047	G=	0.271	S=	0.560	R=	0.105	D=	0.017
				S+=	0.682				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.072	0.014	0.043	*0.006*	0.031	0	0.051	*0.002*	0.047
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.189	0.036	0.113	0.015	0.081	0	0.135	0.006	0.124
4: A1dor	0.219	0.041	0.131	0.017	0.094	0	0.156	0.007	0.143
5: A1	0.265	0.050	0.158	0.020	0.113	0	0.188	0.009	0.173
6: A2dor	0.199	0.037	0.119	0.015	0.085	0	0.141	*0.007*	0.130
7: A2	0.400	0.075	0.239	0.031	0.171	0	0.284	0.013	0.262
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	**0.612**	0.115	0.366	0.047	0.261	0	**0.435**	0.020	**0.401**

Table A4.9 Eigenanalysis for FZ 97-98

Stage matrix (FZ 97-98):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.007	0	0.052	0	0.531
2: NRdor	0	0	0.182	0	0	0	0	0	0
3: NR	0.250	0.167	0.455	0	0	0	0.045	0	0.050
4: A1dor	0	0	0	0	0.125	0	0	0	0
5: A1	0	0	0.182	0.333	0.438	0	0.136	0	0.050
6: A2dor	0	0	0	0	0	0	0.136	0	0
7: A2	0	0	0.182	0	0.438	0	0.500	0	0.300
8: A3dor	0	0	0	0	0	0	0	0	0.100
9: A3	0	0	0	0	0	0	0.182	0	0.500

Lambda, λ 0.9312 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.202	0.151	1.00	1.54
2: NRdor	0.061	0.026	0.42	1.00
3: NR	0.111	0.132	2.33	1.83
4: A1dor	0.030	0.022	1.00	1.00
5: A1	0.162	0.163	2.81	1.78
6: A2dor	0	0.046	0	1.00
7: A2	0.222	0.314	2.86	2.00
8: A3dor	0.010	0.014	0	1.00
9: A3	0.202	0.132	3.82	2.00
Total N	99			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.024	0	0	0	*0.001*	0	0.008	0	0.032
2: NRdor	0	0	*0.005*	0	0	0	0	0	0
3: NR	0.040	*0.005*	0.064	0	0	0	0.015	0	0.007
4: A1dor	0	0	0	0	0.009	0	0	0	0
5: A1	0	0	0.031	0.009	0.092	0	0.055	0	0.009
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.031	0	0.094	0	**0.205**	0	0.052
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	**0.100**	0	**0.115**
Sum	0.064	0.005	0.130	0.009	0.195	0.000	0.382	0.000	0.215
F=	0.040	G=	0.295	S=	0.514	R=	0.137	D=	0.014
				S+=	0.665				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.064	0.011	0.056	0.009	0.070	0.020	0.133	0.006	0.056
2: NRdor	0.027	*0.005*	0.023	*0.004*	0.029	0.008	0.056	*0.003*	0.024
3: NR	0.149	0.026	0.130	0.022	0.162	0.045	0.310	0.014	0.131
4: A1dor	0.065	0.011	0.056	0.009	0.070	0.020	0.134	0.006	0.057
5: A1	0.180	0.031	0.157	0.026	0.195	0.055	**0.375**	0.017	0.158
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0.184	0.031	0.160	0.027	0.199	0.056	**0.382**	0.017	0.161
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0.245	0.042	0.214	0.036	0.265	0.074	**0.509**	0.023	0.215

Table A4.10 Eigenanalysis for GC 95-96

Stage matrix (GC 95-96):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.188	0	2.246	0	224.725
2: NRdor	0	0	0.077	0	0	0	0	0	0
3: NR	0.250	0	0.500	0	0.259	0	0	0	0
4: A1dor	0	0	0	0	0.111	0	0	0	0
5: A1	0	0	0.308	0	0.370	0	0.235	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.115	0	0.259	0	0.706	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	0.059	0	1.000

Lambda, λ 1.6046 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.053	0.721	1.00	1.54
2: NRdor	0	0.008	0	1.00
3: NR	0.347	0.175	5.02	2.00
4: A1dor	0	0.004	0	1.00
5: A1	0.360	0.051	7.25	1.59
6: A2dor	0	0	0	1.00
7: A2	0.227	0.037	28.80	3.40
8: A3dor	0	0	0	1.00
9: A3	0.013	0.004	371.68	infinity
Total N	75			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.036	0	0	0	*0.001*	0	0.012	0	0.115
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	**0.129**	0	0.063	0	*0.009*	0	0	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	0.056	0	0.019	0	*0.009*	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.083	0	0.054	0	0.107	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	**0.116**	0	**0.191**
Sum	0.165	0.000	0.201	0.000	0.084	0.000	0.244	0.000	0.306
F=	0.129	G=	0.437	S=	0.416	R=	0.018	D=	0.000
				S+=	0.434				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.165	*0.002*	0.040	*0.001*	0.012	0	0.009	0	*0.001*
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.828	0.010	0.201	0.004	0.058	0	0.043	0	0.004
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	1.196	0.014	0.290	0.006	0.084	0	0.061	0	0.006
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	**4.752**	0.055	1.154	0.023	0.335	0	0.244	0	0.024
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	**61.332**	0.714	**14.893**	0.298	4.318	0	3.145	0	0.306

Table A4.11 Eigenanalysis for GC 96-97

Stage matrix (GC 96-97):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.284	0	0.738	0	44.758
2: NRdor	0	0	0.217	0	0	0	0	0	0
3: NR	0.250	0	0.348	0	0.136	0	0	0	0
4: A1dor	0	0	0	0	0.091	0	0	0	0
5: A1	0.014	0	0.304	0.400	0.091	0	0.091	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.130	0	0.636	0	0.545	0	0.500
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0.045	0	0.364	0	0.500

Lambda, λ 1.5954 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.779	0.718	1.00	1.54
2: NRdor	0.006	0.020	0	1.00
3: NR	0.067	0.148	4.42	1.53
4: A1dor	0.015	0.002	2.54	1.00
5: A1	0.064	0.040	10.12	1.10
6: A2dor	0	0	0	1.00
7: A2	0.064	0.052	18.70	2.20
8: A3dor	0	0	0	1.00
9: A3	0.006	0.019	49.39	2.00

Total N 344

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.043	0	0	0	*0.002*	0	0.007	0	**0.144**
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	**0.135**	0	0.039	0	0.004	0	0	0	0
4: A1dor	0	0	0	0	*0.002*	0	0	0	0
5: A1	0.017	0	0.078	*0.002*	0.006	0	0.008	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.061	0	0.082	0	0.090	0	0.030
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0.015	0	**0.158**	0	0.079
Sum	0.195	0.000	0.177	0.002	0.111	0.000	0.263	0.000	0.253
F=	0.152	G=	0.546	S=	0.258	R=	0.042	D=	0.002
				S+=	0.302				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.195	0.006	0.040	*0.001*	0.011	0	0.014	0	0.005
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.859	0.024	0.178	*0.003*	0.048	0	0.062	0	0.023
4: A1dor	0.494	0.014	0.102	*0.002*	0.028	0	0.036	0	0.013
5: A1	1.970	0.055	0.407	0.006	0.111	0	0.142	0	0.052
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	**3.639**	0.102	0.751	0.012	0.205	0	0.263	0	0.096
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	**9.613**	0.270	**1.985**	0.031	0.541	0	0.694	0	0.253

Table A4.12 Eigenanalysis for GC 97-98

Stage matrix (GC 97-98):

	1	2	3	4	5	6	7	8	9
1: Sd	0.350	0	0	0	0.236	0	1.492	0	134.740
2: NRdor	0	0	0.487	0	0	0	0	0	0
3: NR	0.250	0	0.359	0	0.143	0	0.067	0	0.200
4: A1dor	0	0	0	0	0.357	0	0	0	0
5: A1	0	0	0.141	0	0.286	0	0.167	0	0.300
6: A2dor	0	0	0	0	0	0	0.233	0	0
7: A2	0	0	0.013	0	0.214	0	0.533	0	0.400
8: A3dor	0	0	0	0	0	0	0	0	0.100
9: A3	0	0	0	0	0	0	0	0	0

Lambda, λ 0.7983 (approximate)

Stage	Initial	Stable	RV	Avg. residence
1: Sd	0.446	0.350	1.00	1.54
2: NRdor	0.020	0.149	0	1.00
3: NR	0.311	0.244	1.79	1.56
4: A1dor	0.008	0.043	0	1.00
5: A1	0.056	0.097	4.75	1.40
6: A2dor	0	0.026	0	1.00
7: A2	0.120	0.090	9.07	2.14
8: A3dor	0	0	0	1.00
9: A3	0.040	0	175.57	1.00
Total N	251			

Elasticities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.075	0	0	0	*0.014*	0	0.082	0	0
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.095	0	0.096	0	*0.015*	0	*0.007*	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0	0	**0.099**	0	0.080	0	0.043	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	0	0	0.018	0	**0.114**	0	**0.264**	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	0	0	0	0	0	0	0	0	0
Sum	0.170	0.000	0.213	0.000	0.222	0.000	0.395	0.000	0.000
F=	0.095	G=	0.326	S=	0.514	R=	0.065	D=	0.000
				S+=	0.579				

Sensitivities: (approximate)

	1	2	3	4	5	6	7	8	9
1: Sd	0.170	0.072	0.119	*0.021*	0.047	*0.013*	0.044	0	0
2: NRdor	0	0	0	0	0	0	0	0	0
3: NR	0.305	0.130	0.213	0.038	0.084	*0.023*	0.078	0	0
4: A1dor	0	0	0	0	0	0	0	0	0
5: A1	0.807	0.344	0.563	0.100	0.222	0.061	0.207	0	0
6: A2dor	0	0	0	0	0	0	0	0	0
7: A2	1.540	0.656	1.075	0.190	0.425	0.116	0.395	0	0
8: A3dor	0	0	0	0	0	0	0	0	0
9: A3	**29.817**	**12.700**	**20.811**	3.677	8.222	2.239	7.652	0	0

Appendix 5. Fertilizer and Growing Mix Analyses

Sierra 17-6-10, Plus Minors Controller Release Fertilizer
Scotts—Sierra Horticultural Products, Marysville, OH

Component	Percentage (%)
Total nitrogen	17
Available phosphoric acid (P_2O_5)	6
Soluble potash (K_2O)	10
Calcium (Ca)	1.5
Magnesium (Mg)	1.0
Sulfur (S)	4.0
Boron (B)	0.02
Copper (Cu)	0.05
Iron (Fe)	0.40
0.13% chelated iron	
Manganese (Mn)	0.10
Molybdenum (Mo)	0.001
Zinc (Zn)	0.05

Big KMart K Gro Best, All Purpose Plant Food

Component	Percentage (%)
Total nitrogen	15
Available phosphorus (P_2O_5)	30
Soluble potash (K_2O)	15
Boron (B)	0.02
Copper (Cu) (soluble)	0.07
Iron (Fe) (chelated)	0.15
Manganese (Mn) (chelated)	0.05
Molybdenum (Mo)	0.0005
Zinc (Zn) (soluble)	0.06

Sunshine All-Purpose Growing Mix
Sun Gro, Bellevue, WA

85-95% Canadian Sphagnum Peat Moss
Perlite
Dolomitic limestone to adjust pH

VITA

Maureen Cunningham was born in Oak Ridge, Tennessee, on July 18, 1953. She attended St. Mary's School in Oak Ridge, Catholic High School in Knoxville, and graduated from Oak Ridge High School in June, 1971. She earned a Bachelor of Arts degree with high honors with a major in Botany in December, 1976, from the University of Tennessee, Knoxville (UT-K). After working as a biological technician for the Tennessee Valley Authority in the Forestry Resources Group, where she was involved in strip mine revegetation projects, she entered the Master of Science program in Botany at UT-K, in September 1980. She completed the Master's program in May, 1983. In that same year she co-founded a native plant nursery, one of the first in the southeastern U.S., which operated primarily through mail order from 1983-1989.

In May 1986, she began working for UT-K at Oak Ridge National Laboratory (ORNL). Her five years of association with ORNL in the Environmental Sciences Division involved research on nitrogen use efficiency in short rotation woody crops for biofuels, as well as natural resource management, rare plant surveys, and wetland surveys on the Department of Energy's Oak Ridge Reservation. In May 1991 she joined the staff of Science Applications International Corporation (SAIC) as an environmental scientist working on environmental compliance projects, including Superfund Site remediation, environmental assessment, ecological risk assessment and rare species compliance guidelines. Clients included the Department of Energy and the Department of Defense.

In September, 1993 Ms. Cunningham returned to UT-K to pursue the Doctorate of Philosophy in Ecology, taking coursework while continuing to work part-time at SAIC. In June 1995, she began full time work on her field and greenhouse research project on population biology of a rare plant species, *Aureolaria patula*. In June 1996, she was appointed to the Department of Energy's Laboratory Graduate Research Participation Program at ORNL, which provided support for her research. The doctoral degree in Ecology and Evolutionary Biology was awarded in May, 2000.