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The Rare Perennial *Balduina atropurpurea* (Asteraceae) at Fort Stewart, Georgia

by
David A. Lincicome

U.S. military installations are refuges to many threatened and endangered ecosystems and species. They are also sites of intensive military training and testing. The U.S. Army is committed to conservation of biological diversity on its lands through the adoption of comprehensive threatened, endangered, and sensitive species (TES) management regulations and initiatives. These regulatory guidelines go beyond single species management by placing TES management in an ecosystem management perspective.

This report discusses the ecology and biology of *Balduina atropurpurea*, a TES associated with Red-cockaded Woodpecker habitat at Fort Stewart. The objectives of the study were to provide baseline information on *B. atropurpurea's*: population locations and sizes; density, dispersion, and number of individuals; variation in vegetative condition; variation in reproductive condition; viability of seeds; vegetative and reproductive phenology; and habitat quality at Fort Stewart as of 1996. This baseline information is needed to begin the design of a demographic monitoring program, determine management needs, provide initial guidance on prioritization of populations for conservation and prioritization of management prescriptions for each population, and begin the assessment of the effects of RCW management and military training and testing on the persistence of *B. atropurpurea* at Fort Stewart.

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U.S. military installations are refuges to many threatened and endangered ecosystems and species. They are also sites of intensive military training and testing. The U.S. Army is committed to conservation of biological diversity on its lands through the adoption of comprehensive threatened, endangered, and sensitive species (TES) management regulations and initiatives. These regulatory guidelines go beyond single species management by placing TES management in an ecosystem management perspective.

This report discusses the ecology and biology of *Balduina atropurpurea*, a TES associated with Red-cockaded Woodpecker habitat at Fort Stewart. The objectives of the study were to provide baseline information on *B. atropurpurea's*: population locations and sizes; density, dispersion, and number of individuals; variation in vegetative condition; variation in reproductive condition; viability of seeds; vegetative and reproductive phenology; and habitat quality at Fort Stewart as of 1996. This baseline information is needed to begin the design of a demographic monitoring program, determine management needs, provide initial guidance on prioritization of populations for conservation and prioritization of management prescriptions for each population, and begin the assessment of the effects of RCW management and military training and testing on the persistence of *B. atropurpurea* at Fort Stewart.

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Executive Summary

Balduina atropurpurea is a rare wetland perennial plant occurring in large, healthy, known populations at Fort Stewart, Georgia. This biologically significant plant was selected as a target species for research focusing on activities for enhancing the survival and recovery of threatened, endangered, and sensitive plant species (TES) on military lands. A conservation management approach was outlined emphasizing a demographic trend analysis, factor resolution, and management prescription framework that may provide the necessary biological, ecological, and genetic information to make appropriate management decisions and assessments in a timely and cost-effective manner. This study was designed to document the baseline condition of *B. atropurpurea* populations at Fort Stewart as of 1996 in support of future demographic monitoring and experimental studies on this species. Reproductive data used in the analysis was from 1995.

Twenty-seven populations were mapped using a global positioning system (GPS) and Geographic Resources Analysis Support System (GRASS) geographic information system (GIS) software. Randomized field sampling was used to estimate plant density and dispersion, population size, vegetative and reproductive condition of flowering individuals, and the environmental condition of each population in 1996. Principal components analysis (PCA) and descriptive discriminant analysis (DDA) were used to assess the morphological relationship and degree of separation among the populations with respect to four vegetative and reproductive variables. In early 1996, greenhouse trials of seed viability were conducted using seeds collected in the fall of 1995.

The 27 populations studied on Fort Stewart contained an estimated 10,477 to 44,299 individuals and encompassed a total of 25.9 hectares—a larger population size and area than initially expected. Seven populations had more than 1,000 individuals and six populations were larger than 1 hectare. Genet* density was low with 0.30 ± 0.04 genets/m^2. Three measures of dispersion indicated an aggregated dispersion of individuals. The vegetative condition and general health of the

* Genet: A genetically unique individual arising from a seed. Also a solitary rosette/stem or a cluster of rosettes/stems.

individuals was not severely threatened by disease or predation. Based on the PCA and DDA analyses, little or no differentiation among the populations was detected (λ=0.638, τ^2=0.106, classification error rate = 0.87). This result was consistent with previous genetic analyses on this species.

Seed production and mean seed weight were relatively low and seed viability was relatively high compared to other composites. Approximately 60% of the genets and ramets* flowered in 1995 with an average of 4±0.19 inflorescences per genet and 3±0.10 inflorescences per ramet. Fifty-six percent of the ramets flowered in 1996. There was an average seed set of 0.30±0.04, representing an average of 36±4.65 mature seeds per inflorescence. The average individual seed mass was 1.2±0.10 mg. The average proportion of seedling emergence was 0.75±0.05 in the greenhouse and the average seedling emergence rate, or time till 50% of the seedlings emerged, was 4±0.17 days. Seed set appeared to be related more closely to population size than plant size.

The qualitative assessment of the environmental condition of the *B. atropurpurea* populations characterized the populations as having been influenced by natural disturbance (52% of quadrats), having a low degree of disturbance (64% of quadrats), and having a high relative light level (69% of quadrats) overall. Sixty-seven percent of the populations were dominated by quadrats characterized by natural disturbance and 78% of the populations were dominated by quadrats characterized by a low degree of disturbance and by a high relative light level. In relation to site quality, the main concern was for populations with a high degree of disturbance and/or low relative light level. A nearly even number of quadrats were characterized as having natural or human disturbance. The data suggested that human activity was more likely to result in a greater degree of disturbance, and that human disturbance, primarily military vehicle traffic, may be a threat to the integrity of *B. atropurpurea* wetland sites.

It is recommended that these wetland sites be protected from military vehicle disturbance, a monitoring program be implemented, and a fire regime be restored to all sites. Furthermore, as the need arises and resources permit, it is recommended that additional research on habitat characterization, pollination biology, seed ecology, genetic variation, vegetative and reproductive phenology, vegetative reproduction, predation, and disturbance effects on growth and reproduction be conducted to assist in the management of this species.

* Ramet: A genetically identical individual arising from vegetative propagation. Also a rosette/stem within a cluster.

Foreword

This study was conducted for the Strategic Environmental Research and Development Program (SERDP), under the Threatened and Endangered Species (TES) Program, Thrust Area: Enhancing the Recovery of TES Plants; HQ FORSCOM, MIPR E87950340, titled "Inventory and Monitoring of Rare Plant Species,"; and Fort Stewart. The technical monitors were Dr. Femi Ayorinde, Conservation Program Manager at the SERDP office; Dr. Bert Bivings, HQ FORSCOM, AFPI-ENE; and Linton L. Swindell, Fort Stewart Fish and Wildlife Branch, AFZP-DEV-W.

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This work was performed by the Natural Resource Assessment and Management Division (LL-N) of the Land Management Laboratory (LL), U.S. Army Construction Engineering Research Laboratories (USACERL). The USACERL principal investigator was Dr. Alison Hill. Dr. William D. Severinghaus is Operations Chief, CECER-LL. The USACERL technical editor was Gloria J. Wienke, Technical Information Team.

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1 Introduction

Background

United States military installations are refuges to many threatened and endangered ecosystems and species. However, they are also active sites of intensive military training and testing. These training and testing exercises are often perceived to be in conflict with the maintenance of healthy ecosystems and/or species populations. On the contrary, military installations often contain some of the largest and healthiest intact examples of natural communities. Many of these communities benefit from the disturbances created by military training and testing. Compliance with the Endangered Species Act (ESA) places responsibility on the military to conserve rare species and their associated ecosystems. The U.S. Army has accepted this responsibility and is committed to conservation of biological diversity on its lands through the adoption of comprehensive threatened, endangered, and sensitive species (TES) management regulations and initiatives (U.S. Department of the Army [DA] 1992; Army Regulation [AR] 200-3 Ch. 11). These regulatory guidelines go beyond single species management by placing TES management in an ecosystem management perspective (Department of Defense [DoD] Memorandum DUSD[ES]/EQ-CO, 8 August 1994). In many cases, TES species distributions cross administrative or political boundaries and if proper management is to occur, especially if metapopulation dynamics is important, ecosystem management is a necessity. The aim of ecosystem management is to restore and maintain the function, structure, and species composition of an ecosystem while recognizing that change is a natural process within historical limitations (Trame and Tazik 1995). The ecosystem management perspective acknowledges the human existence in ecosystems and incorporates our values into management goals (Agee and Johnson 1988; Pickett, Parker, and Fielder 1992; Howald 1993; Grumbine 1994; Trame and Tazik 1995). Ecosystem management supports our country's need for natural resource conservation as well as the need for military training and testing activities.

The Army's Threatened and Endangered Species Research and Development User Group selected Fort Stewart Military Reservation in Georgia as the model installation for TES research in the Southeastern United States. Fort Stewart contains large, healthy populations of the rare wetland perennial *Balduina atropurpurea*. Fort Stewart also contains approximately 165 active Red-cockaded

Woodpecker (RCW) cluster sites, which have brought about changes in the management and military training activities within RCW habitat. Any action to restore or maintain RCW habitat must also be compatible with other native species, including *B. atropurpurea*. Environmental managers currently lack baseline information needed to determine the management needs and activites for *B. atropurpurea*. This research begins to provide that baseline information.

Objective

This autecological study of *B. atropurpurea* was conducted at Fort Stewart, GA, during the summers of 1995 and 1996. The overall objective of the study was to provide baseline information (as of 1996) on *B. atropurpurea's*:

1. population locations and sizes
2. density, dispersion, and number of individuals
3. variation in vegetative condition
4. variation in reproductive condition
5. viability of seeds
6. vegetative and reproductive phenology, and
7. environmental condition (habitat quality).

This baseline information is needed to begin the design of a demographic monitoring program to estimate long-term population trends and determine the management needs of *B. atropurpurea*, and to begin the assessment of the effects of RCW management and military training and testing on the persistence of *B. atropurpurea* at Fort Stewart. Furthermore, it will provide initial guidance on prioritization of populations for conservation and prioritization of specific management activities for each population.

Approach

A review of existing literature on rare plant conservation, ecosystem management, and the biology and ecology of *B. atropurpurea* was conducted. Interviews and consultations with experts in academia (Colorado State University, Georgia Southern University, University of Georgia, University of Illinois, and South Georgia College); government agencies (U.S. Fish and Wildlife Service [USFWS], Georgia Natural Hertiage program [GNHP], U.S. Army Construction Engineering Research Laboratories [USACERL], and the natural resource personnel at Fort Stewart); and private organizations (The Nature Conservancy [TNC] and The

Atlanta Botanical Garden) familiar with the biology, ecology, and conservation of *B. atropurpurea* were also conducted.

Based on the literature, interviews, and consultations, an approach (see Figure 1 in Chapter 2) to the conservation management of *B. atropurpurea* was outlined. Within the context of this conservation management approach, and based on the present knowledge of *B. atropurpurea,* an intensive survey based on population sampling was designed to document aspects of the autecology of the study species at Fort Stewart.

The overall strategy adopted to answer the principal research question (see Table 1) was composed of four parts. First, the *B. atropurpurea* populations were mapped using Global Positioning System (GPS) and Geographic Information System (GIS) technologies so the exact location, dispersion, and dimension of each population were known. Second, field sampling at random points within each population was used to estimate the density, population size, dispersion, vegetative and reproductive condition of flowering individuals, and general environmental condition of the populations. Third, *ex situ* (greenhouse) methods were used to test the viability of seeds collected from individuals sampled in the field. Last, principal components analysis (PCA) and descriptive (canonical) discriminant analysis (DDA) were used to reveal the relationship and degree of separation among the populations with respect to four vegetative and reproductive characters.

The field sampling for each study task (Table 1) was conducted during the peak flowering period of two consecutive growing seasons (1995 and 1996) so that plants were easily found and seeds collected. The seeds were collected only at the end of the growing season in 1995 and propagated during the following winter and early spring of 1996.

Mode of Technology Transfer

The information in this report will be provided to Fort Stewart, GA, natural resource personnel to aid in the management of *B. atropurpurea*. This work is supplemented by work from C. Helton (in prep), a survey of Fort Stewart for additional *B. atropurpurea* populations, and Halward, Hill, and Shaw (in prep), an analysis of the genetic diversity within and among populations of *B. atropurpurea* at Fort Stewart.

Table 1. The principal research question and task area specific research questions for the *B. atropurpurea* study at Fort Stewart in 1995 and 1996.

Principal Research Question	**• What is the distribution and abundance of individuals, and the vegetative and reproductive condition of flowering individuals at each Balduina atropurpurea population within Fort Stewart?**
Population Data	• What is the location and physical extent of each population? — On what soil types do the populations occur?
	• What is the number of genets for each population (population size)?
	• What is the density of genets in each population? — Does the density of genets vary among populations?
	• What is the dispersion of genets in each population? — Does the dispersion of genets vary among populations?
Vegetative Data	• What is the vegetative condition of flowering individuals in each population?
Reproduction	• What is the density of inflorescences in each population? — Does the density of inflorescences vary among populations?
	• What is the condition of floral production in each population? — Do floral characters vary among populations?
	• What is the seed production in each population? — Does the seed production vary among populations?
	• What proportion of the seed production is viable? — Does the proportion of viable seeds vary among populations?
Phenology	• When is the beginning, peak, and completion of germination, rosette growth, stem elongation (bolting), flowering, seed dispersal and winter dormancy?
Environmental Data	• What is the environmental condition of each population, based on the frequency of disturbance type, disturbance degree, and light level classes?
	• Is there any relationship among disturbance type, disturbance degree, and light level?
	• Does the density of genets and inflorescences differ among disturbance type, disturbance degree, and light level classes?

Principal Research Question	• **What is the distribution and abundance of individuals, and the vegetative and reproductive condition of flowering individuals at each Balduina atropurpurea population within Fort Stewart?**
Discriminant Analysis	• Are there simultaneous population mean differences (centroid separation) with respect to the number of ramets per genet, number of stems per genet, number of inflorescences per genet, and mean stem height per genet? — Can these differences be meaningfully characterized by some linear combination of the four variables? — Can the linear combination of variables be meaningfully defined? — Which of the four variables contributes most to the population mean differences? — In how many dimensions can this population mean separation be represented? — What population separation configuration is produced by the population means?

2 TES Research and the Study Site

The Role of Ecological Research in Plant Conservation and Management

An integrated conservation strategy can help achieve plant conservation in a timely and cost-effective manner (Falk 1992; Given 1994; Schemske et al. 1994; National Research Council [NRC] 1995; Carroll et al. 1996). This integrated strategy entails land acquisition and protection, management, onsite and offsite research, propagation, and genebanking (Falk 1992). For the military, the emphasis should first be on increasing the knowledge base of species biology and on increasing population size and stability (if necessary) since the land is already in possession.

Because very little is known about the biological, ecological, and genetic characteristics of most rare plants (Falk 1987; Fahselt 1988; Holsinger and Gottlieb 1991; Owen and Rosentreter 1992; Howald 1993; Allen 1994; Given 1994; Schemske et al. 1994; Pavlik 1994, 1996), biologists are not in the position to adequately manage rare plants for conservation. Moreover, Fiedler and Ahouse (1992), Given (1994), Schemske et al. (1994), NRC (1995), and Carroll et al. (1996) emphasize that understanding why a species is rare is a necessity for developing conservation plans. However, in a review of 98 USFWS recovery plans for individual species between 1980 and 1992, Schemske et al. (1994) found that most plans lacked sufficient biological information to assess population dynamics and the proposed demographic research was not designed to determine the biological status or the critical life-history stages of the populations. The NRC (1995) and Carroll et al. (1996) reached a similar conclusion. Therefore, the plans were inadequate for determining recovery management. Successful management of TES plants requires a basic understanding of the species biology, ecology, reproduction, population biology, and genetic structure (Falk 1987, 1992; Holsinger and Gottlieb 1991; Falk and Olwell 1992; Given 1994; Schemske et al. 1994; Guerrant 1996; Pavlik 1996).

Massey and Whitson (1980), Given (1994), Pavlik (1994), and Schemske et al. (1994) outlined components of a conservation strategy that have been adapted into a conservation management approach (Figure 1). This approach permits the determination of management needs in a timely and cost-effective manner. Inventories are the first step in identifying the geographic distribution of species by noting their absence or presence. Sometimes count data and habitat preference at

various locations can be used to characterize species distribution (Owen and Rosentreter 1992; Given 1994).

Once an inventory has been completed and the locations of rare species are known, more rigorous survey work can proceed. Surveys may map populations, identify and assess threats (including stress and competition), identify biologically critical habitat, count plant numbers, and examine plant growth and reproduction (plant size, flowering, and fruiting) (Massey and Whitson 1980; Palmer 1987; Sawyer and Andre 1990; Given 1994; Pavlick 1994). Surveys provide specific details on population and community parameters by using sampling techniques and statistical analyses. Surveys lead to identification of problems or aspects of species biology that deserve more detailed analysis (Given 1994).

More sophisticated and detailed study questions should arise from the baseline information provided by less sophisticated information gathering (Given 1994). Surveys are important because they set the stage for demographic studies that provide more direct insight into management needs. The design of a demographic study depends on the population extent and size, density and dispersion of individuals, and variability of the species characteristics and habitat (Travis and Sutter 1986). All of this information can be gathered from a rigorous survey. Once the initial state of the populations is known, monitoring is the next logical step to identify the timing and causes of poor performance and provide specific management recommendations (Massey and Whitson 1980; Given 1994).

Schemske et al. (1994) and Pavlik (1994) have provided the most detailed discussion of the demographic monitoring approach. Pavlik has divided demographic

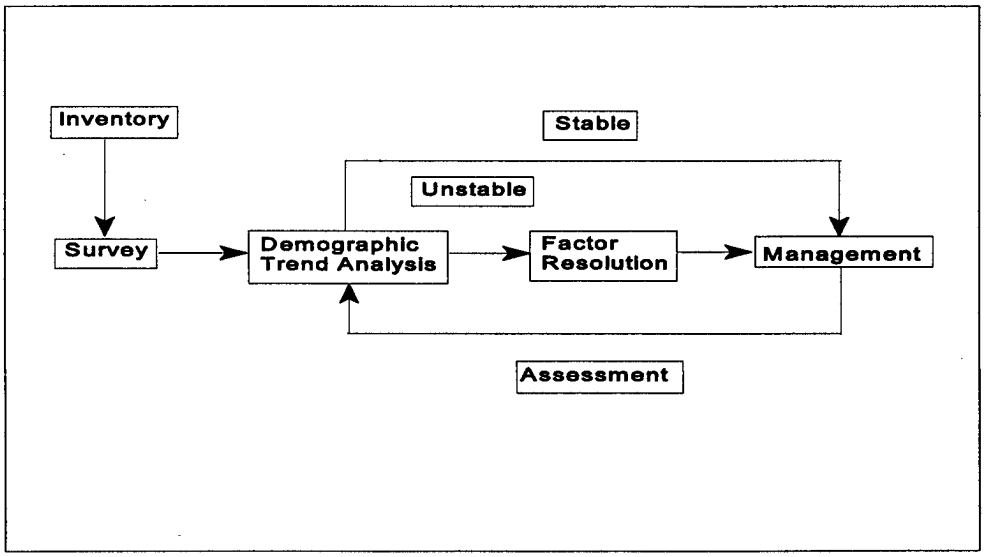


Figure 1. Schematic diagram of the TES conservation management approach.

monitoring into two activities: trend analysis and factor resolution. Trend analysis is used to determine which populations of a species require management intervention. Whether populations are decreasing, stable, or increasing is a key question to be addressed (Menges 1986, 1991; Given 1994; Pavlik 1994; Schemske et al. 1994). Trend analysis also identifies which life-history stage is limiting the population growth or stability. The most common analyses used are the population viability analysis (PVA) (Menges 1986, 1990, 1991) and the Leslie (Leslie 1945) and Lefkovitch (Lefkovitch 1965) matrix population models.

When the population status and critical life-history stage have been determined, factor resolution is then used to determine which factors are limiting that stage's performance. Ultimately, this will indicate what type of management is needed to stabilize or increase a population (Massey and Whitson 1980; Menges 1986; Travis and Sutter 1986; Palmer 1987; Schemske et al. 1994; Pavlik 1994). The appropriate experimental approach for factor resolution should be determined by characteristics of the life-history stage and the nature of the specific question being asked. The factors affecting a life-history stage may be intrinsic (demographic characteristics, breeding system, levels of genetic variability, etc.) or extrinsic (biotic and abiotic components of the environment, human disturbance) (Pavlik 1994).

The most important information needed to determine a management strategy is the demographic trends of the populations and the identification of the critical life-history stage(s) and their limiting factors (Schemske et al. 1994). Population recovery should then be based on *in situ* restoration of the critical demographic processes over a period long enough to ensure population persistence (Pavlik 1994). Demographic monitoring should then be continued to assess management actions and be followed by modification of the management program if needed as shown in Figure 1 (Palmer 1987; Pavlik 1994). A more complete discussion of the TES conservation management approach can be found in Lincicome (1998).

In short, TES plant conservation management requires inventories to determine where species exist, surveys to provide baseline biological and ecological data, demographic trend analysis to identify population stability and identify the critical life-history stage, factor resolution to determine what biotic and abiotic factors are limiting performance in the critical life-history stage and to determine a prescription for a management regime to mitigate the poor performance, and continued monitoring to assess the management — all performed within an ecosystem management context.

Installation and Species Selection

The Army's Threatened and Endangered Species Research and Development User Group selected Fort Stewart Military Reservation in Georgia as the model installation for TES research in the Southeastern United States. The focus of proactive research activities for enhancing survival and recovery of TES species was also guided toward former federal candidate species associated with the Red-cockaded Woodpecker (RCW) (*Picoides borealis*) habitat in an effort to ensure that RCW management is not negatively impacting these TES species (Tazik et al. 1995; Hill and Kirby 1998). After all, management for a target species or site, such as the RCW and its habitats, has broader implications because interrelationships exist between the management of ecosystems, species, and populations. Consequently, management cannot be done independently of habitats and ecosystems (Pickett, Parker, and Fiedler 1992; Given 1994; Grumbine 1994).

Fort Stewart is home of the 24th Infantry Division (Mechanized), an estimated 165 active RCW cluster sites (USACERL 1994), and 13 former candidate plant species (TNC 1995a). The longleaf pine/wiregrass ecosystem, characteristic of the installation, is also one of the most threatened ecosystems in the world (Noss 1989). Concern over the endangered RCW has brought about changes in the management and military training activities within designated RCW Habitat Management Units (HMUs). Because of the recommended size of these HMUs (100,00 to 150,00 acres for 500 RCW groups in the recovery population), it would have been risky to use only narrow, single-species management objectives to make all management decisions. Therefore, any action to restore or maintain RCW habitat must also be compatible with the other native species of the community (TNC 1995b).

The rare perennial, *Balduina atropurpurea*, was selected as a target species for research focusing on activities for enhancing the survival and recovery of TES species. Because of its biological significance as an endemic of a three-species genus; the lack of autecological information; its occurrence in RCW habitat; the presence of the largest, healthiest known populations on Fort Stewart; and its suitability for testing the application of the TES conservation management approach, an autecological study was undertaken on this species.

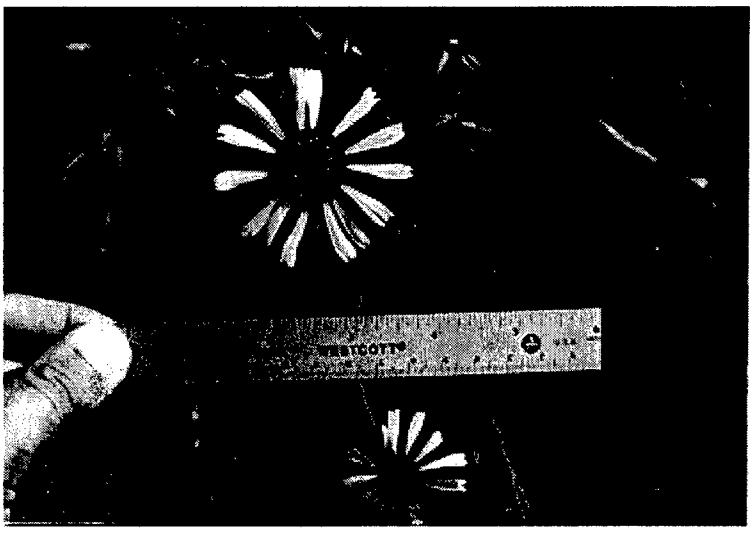
Species Description

Balduina atropurpurea Harper is a former federally listed C2 species endemic to the coastal plain of the Southeastern United States. A former C2 federal listing by USFWS meant that there was insufficient data on the biological vulnerability of this

species to warrant listing as endangered or threatened although such a listing was possibly appropriate. It was given a G2G3 global ranking by The Nature Conservancy Natural Heritage Inventory (Smith 1994, TNC 1995b). A G2 ranking is assigned to those elements imperiled globally due to rarity or some factor(s) making it very vulnerable to extinction throughout its range (6 to 20 occurrences or few remaining individuals or acres). A G3 ranking is assigned to those elements either very rare and local throughout its range or found locally in a restricted range or due to other factors making it vulnerable to extinction throughout its range (21 to 100 occurrences). Historically, the distribution of *B. atropurpurea* was from southeastern North Carolina south to northeastern Florida, then west through the Florida panhandle to southeastern Alabama. Currently, its known range extends from central South Carolina (Fort Jackson Army Installation) (Nelson and Kelly 1997) south through eastern and south-central Georgia into northeastern Florida. There is also a report of at least one occurrence in Mississippi, which would extend its westward distribution (USDA 1996). Siting of a few individuals in southeastern Alabama has not been verified (Smith 1994; TNC 1995b). In Georgia, where it is listed as state rare, it is historically recorded from 21 counties (Smith 1994; Patrick, Allison, and Krakow 1995; TNC 1995b); however, only 6 counties are currently known to have extant populations (Smith 1994; TNC 1995b). In general, known population numbers have dwindled over the past 15 years, most likely due to site disturbance or lack of management. In fact, only 11 of 39 existing populations had been verified in Georgia during this period (Smith 1994; TNC 1995b). *B. atropurpurea's* largest, healthiest populations are believed to occur on Fort Stewart (TNC 1995a). As of October 1996, there were 29 known populations of *B. atropurpurea* on Fort Stewart, all found between 1992 and 1996 (TNC 1995a, Helton in prep).

B. atropurpurea is a fall flowering, facultative wetland perennial in the Asteraceae family, tribe Heliantheae (Figure 2). It is erect, usually with one stem, sometimes with 2-5 or more branches. The stems are purple-red at the base, pubescent, and 0.5-1.2 m tall. It can reproduce vegetatively from rootstock. The rootstock is short, thick, erect and the roots are fleshy and shallow. Basal leaves are 7-32 cm long and 0.3-1 cm wide while cauline leaves are 3.8-6.2 cm long and 2-6 mm wide. The leaves are linear-spatulate, fleshy, finely pitted, entire and sessile or short petioled. The inflorescences are showy, sunflower-like heads 5-6 cm wide and 2 cm deep. There are 10-15 sterile ray flowers, deep yellow, 3-5 toothed at the apex, 1.6-3.2 cm long and 2.3-4.7 mm wide at apex. These ray flowers surround 30-200 fertile disk flowers, burgundy-purple, imperfect, with a narrowly funnelform throat and shorter tube, 4-7 mm long and 1.2-1.8 mm wide. The involucre is hemispheric to broadly campanulate, receptacle chaffy, chaff united forming an erose honeycomb head. The

A flowering genet.



Two open inflorences: The top infloresecence with outer stigmas and one row of anthers exposed, the bottom infloresecence still opening and just prior to the outer row of anthers emerging.

Figure 2. *Balduina atropurpurea* on Fort Stewart, Georgia.

bracts are green, 3-seriate, ovate, in 3-5 imbricate series. The fruits are dark brown achenes, narrowly oblanceolate, borne singly in each 5- or 6-sided honeycomb cell. Achenes are finely pubescent, capped by a ring of 10-12 narrow, thin scales, and are 1.5-4 mm long and 1.7-3.1 mm wide (Small 1933; Radford, Ahles, and Bell 1973; Cronquist 1980; Godfrey and Wooten 1981; Kral 1983; Wunderlin 1983; Patrick, Allison, and Krakow 1995; TNC 1995a, 1995b).

The flowering period is from mid-August to mid-October with the peak at Fort Stewart from late August through September. Fruiting occurs from October through November.

Parker and Jones (1975) conducted a study on the morphological, anatomical, cytogenetic, and biochemical differences among the three species of *Balduina (B. atropurpurea, B. uniflora, and B. angustifolia)*. They concluded that there was valid specific status among these taxa based on their findings. Furthermore, they concluded that *B. atropurpurea* was self-incompatible and that interspecific hybridization does not occur between the three species. Finally, *B. atropurpurea* has a chromosome number n=18.

Halward, Hill, and Shaw (in prep) examined the relative levels of genetic diversity among and within populations of *B. atropurpurea* at Fort Stewart. The study was limited to the five known populations rediscovered in 1995 (population six was not found). Fifty-nine of the 100 primers screened produced strong amplification products. Of these primers, only 7 (12%) revealed genetic differences among individuals, producing 25 scorable bands. Only 10 of these bands showed variability among individuals. The differences in banding patterns were randomly, and approximately equally, distributed among populations and among individuals within a population. The results of the Randomly Amplified Polymorphic DNA (RAPD) analysis indicated that the five *B. atropurpurea* populations at Fort Stewart were similar in genetic composition. However, the recently discovered populations should be evaluated to determine whether any of these populations contain unique genetic characteristics.

Little is known about *B. atropurpurea's* autecology, demography, or management needs. Consequently, research on its biology, reproduction, management needs, and response to fire season, fire frequency and hydrology are needed (Smith 1994; TNC 1995b).

Site and Setting

Fort Stewart is located entirely within the Coastal Plain physiographic province of the Southeastern United States (Figure 3). Normal climatological conditions at Fort Stewart are characterized by short, mild winters and warm, humid summers. The mean winter temperature is 12 °C and the mean summer temperature is 27 °C. Precipitation is fairly regular throughout the year, but is less pronounced in late fall and winter. Average annual rainfall is approximately 127 cm, with 60% occurring between April and September. The 228-day growing season extends from mid-March to mid-November (TNC 1995a; USDA-SCS 1982). Weather conditions during the 1995 and 1996 study years were characterized by slightly warmer than average temperatures and much lower than normal precipitation, particularly in 1996 (102.1 cm and 76.7 cm, respectively). A more extensive description of Fort Stewart's climate and physical characteristics and *B. atropurpurea*'s habitats can be found in Lincicome (1998).

At the time this study was conducted, there were 28 *B. atropurpurea* populations located in 5 training areas (Echo 10, Echo 11, Echo 16, Echo 17, and Echo 19), four counties (Evans, Liberty, Long, and Tattnal), and within the Taylors Creek drainage system in the west-central portion of Fort Stewart (Figure 4 and Appendix A). Near the end of the 1996 fieldwork, one additional population was discovered by Fort Stewart Fish and Wildlife personnel, bringing the total number of populations to 29; this population was not included in this study.

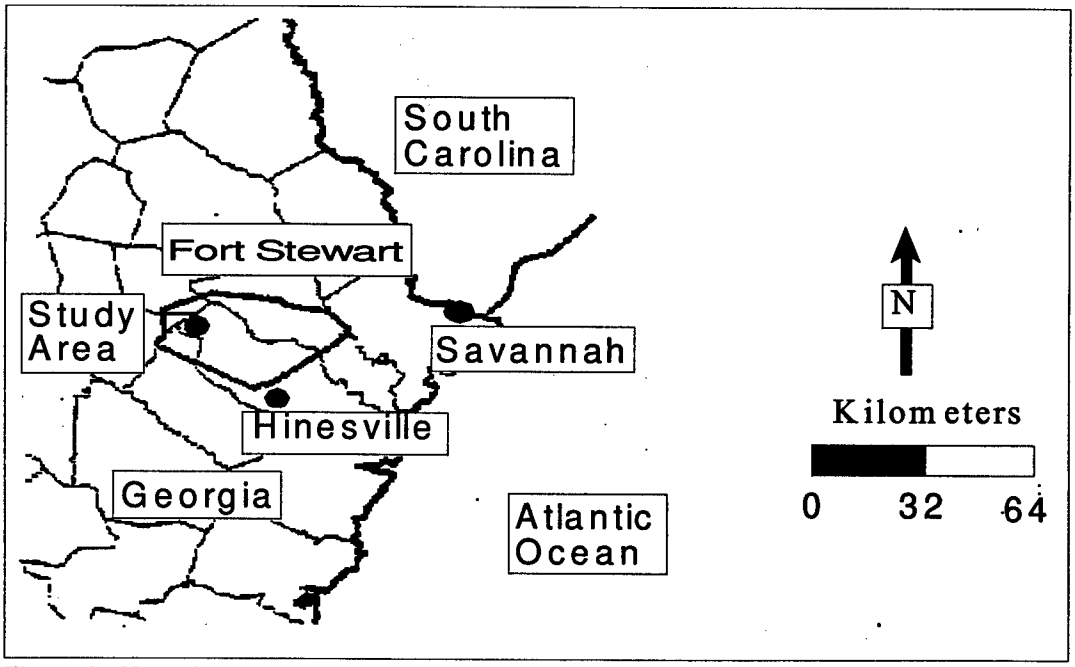


Figure 3. Map of southeastern Georgia showing location of study area within Fort Stewart.

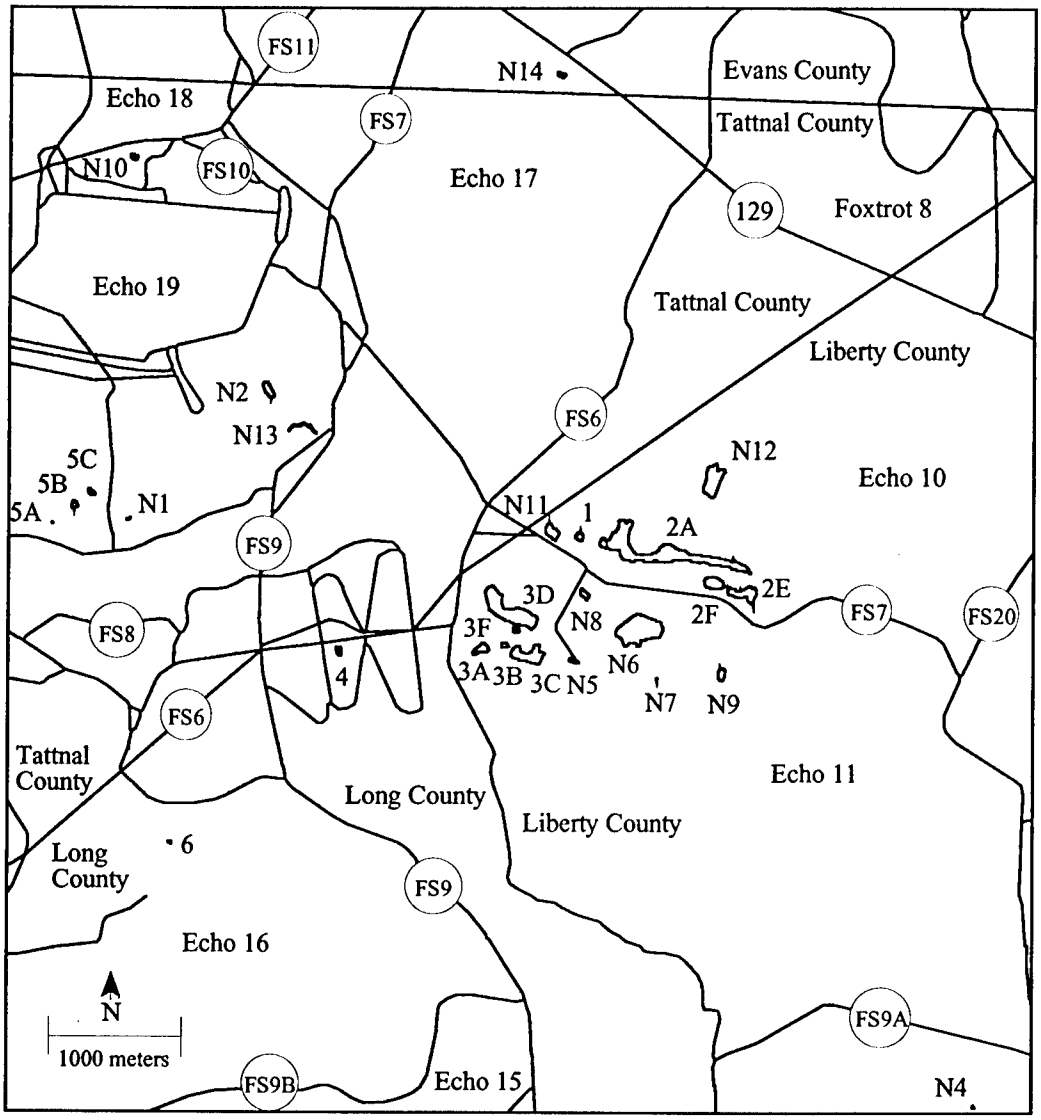


Figure 4. *B. artropurpurea* populations, training area boundaries, county boundaries, and major roads within the Fort Stewart study area.

Approximately two-thirds of the *B. atropurpurea* populations are located in a TNC designated conservation site. Seventeen of the populations (eighteen including the most recently discovered population) are located within the Sandhill Cemetery (Echo 10, Echo 11, and Echo 17), one is located in the Metz Pond Pinelands (Echo 19), and one is located in the Birds Creek (Echo 19) Conservation Sites (Appendix A). Populations 5a, 5b, and 5c are located just west of the Metz Pond Pinelands and populations N2, N3*, and N13 are located just northeast of the Metz Pond Pinelands Conservation Site. Population 6 is located just north of the Long County Point Flatwoods, population 4 is just west of the Sandhill Cemetery, and population N4

* N3 was not located or mapped in 1996.

is between Bethel Cemetery and Bastogne Airstrip Conservation Sites (Appendix A). These conservation sites were designated by TNC as sites of significant biodiversity containing concentrations of rare species and highly intact natural communities (TNC 1995a).

B. atropurpurea occurs in low, wet areas of pitcher plant (*Sarracenia* spp.) bogs; wet pine flatwoods; wet pine savannas; moist, sandy, peaty clearings among slash (*Pinus elliottii*) and longleaf (*P. palustris*) pines; and sandhill seeps with seasonal standing water. This plant typically grows on moist, acidic, sandy soils. In general, it is often associated with an understory of palmetto, saw palmetto, shrub hypericums, ericaceous shrubs, lycopods, xyrids, and pitcher plants (Patrick, Allison, and Krakow 1995; TNC 1995a, 1995b) (see Appendix B).

B. atropurpurea is found within the following habitats on Fort Stewart: cypress savanna, pine savanna, sandhill seeps, edges and openings within wet-mesic and dry-mesic longleaf pine flatwoods, edges of cypress-gum ponds, and edges of wooded blackwater streams (Appendix A) (Helton in prep). Many of these habitats or portions of them resemble what have been called pitcher plant bogs, although *Sarracenia* spp. are not always present. Nonetheless, they have many of the same characteristics. The *B. atropurpurea* populations exist at an average elevation of approximately 35 meters above sea level (Appendix A).

The general characteristics of these habitats have been discussed by various authors. Habitats where *B. atropurpurea* occur can best be described as non-alluvial wetlands. These are communities with variable hydroperiods occurring in basins or depressions, or on slopes, with no connection to above-ground streams or river systems (Sutter and Kral 1994). It is believed that non-alluvial wetlands contain over one-third of the rare plant species in the southeast. Four major environmental variables control the vegetation in these habitats: hydroperiod, fire frequency, presence of organic matter, and source of water (Christiansen 1988; Ewel 1990; Sutter and Kral 1994). Most of these habitats are nutrient limited (Christiansen 1988) and have rainfall or shallow groundwater as the primary water source (Sutter and Kral 1994).

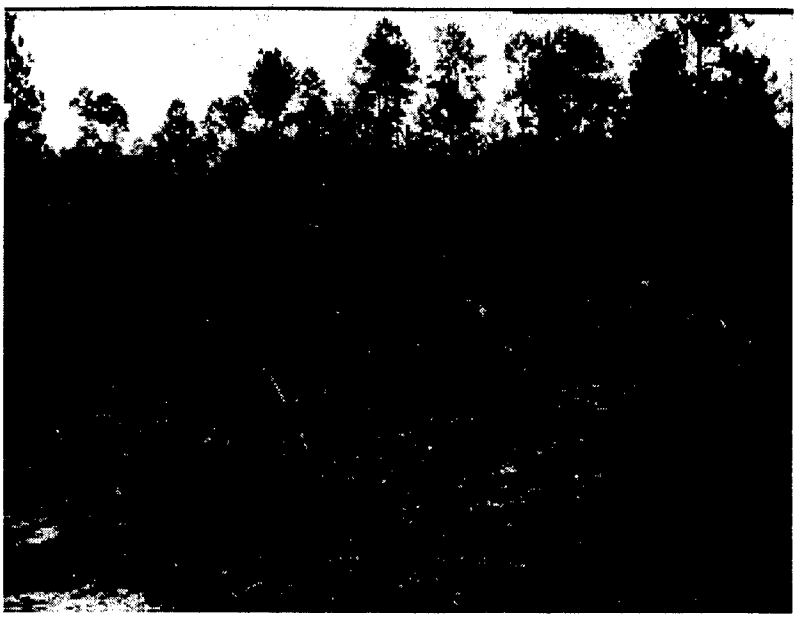
The soils of Fort Stewart developed from unconsolidated Coastal Plain deposits. They are acidic (pH 4.5-5.0) and have low organic matter content (TNC 1995a). *B. atropurpurea* is believed to occur on the following soil series within Fort Stewart: Ellabelle, Fuquay, Leefield, Osier, and Pelham (Appendix A). All of these soils are classified as Ultisols, except Osier which is an Entisol. These soil series have a seasonally high water table.

Soil samples from the top 5 cm of the soil profile were analyzed from all populations of *B. atropurpurea* on Fort Stewart in 1995. All populations occur on acidic soils (pH 3.9 - 5.0) with a sandy loam texture and a relatively low organic matter content (1.0 - 6.7%). Soil nutrient content varied considerably with respect to levels of phosphorous (0.2 - 26.2 mg/kg), potassium (0.1 - 19.1 kg/mg) and iron (14.4 - 349.0 mg/kg) (see Appendix C) (Halward, Hill, and Shaw in prep).

Autumn dry periods are characteristic of the Coastal Plain. The soils of moist pine barrens dry in part from the rapid transpiration by plants with relatively shallow roots; however, near the end of the autumn drought these soils are still wet. It is believed that the soils remain wet from internal drainage through the upland soils above the impervious clay layer into the topographically lower bog habitats over the 6 to 8 week drought. September and October may be critical months for the survival of many moisture-sensitive bog species (Plummer 1963).

Soil moisture is strongly influenced by slight changes in elevation and may change laterally over a distance of only 0.6 - 0.9 m; however, in most pitcher plant habitats, the water gradient is gradual and extends perhaps 30 m into the gently sloping uplands (Plummer 1963). Military off-road vehicle (ORV) tracks and fire breaks are common on Fort Stewart. Both disturbances alter hydrology over short distances. *B. atropurpurea* appears to be sensitive to hydrologic alterations — too wet or too dry — and consequently may be impacted by these disturbances. A ditch as shallow as 0.2 m will usually dry the surface soil to an extent that will eventually eliminate bog species (Folkerts 1982). Military ORV ruts as deep as 0.2 m and 1.25 m wide have been observed on Fort Stewart within *B. atropurpurea* habitats. Military ORV traffic may also physically kill plants via impaction and crushing (Figure 5).

In relation to pitcher plant bogs, most species present are classified as heliophytes — species showing adaptation to bright, sunlit habitats (Plummer 1963; Folkerts 1982). Shaded habitats, whether along woodlands or in areas suffering shrub invasion, may be less productive. *B. atropurpurea* appears to be sensitive to the level of light reaching the forb layer. Observations suggest that *B. atropurpurea* appears to respond positively to opening up the canopy. For example, since 1975, Metz Range has been managed through timber removal and prescribed burns to maintain openness. This appears to be ideal management for *B. atropurpurea*; the largest populations are on Metz Range (Figure 6). Moreover, outside the installation's boundary, *B. atropurpurea* populations are commonly found in open power line right-of-way bogs that receive periodic mowing. Heliophytes are dependent on several natural phenomena that retard succession, including soil acidity coupled with low nutrient levels, anaerobic conditions resulting from frequent saturation,

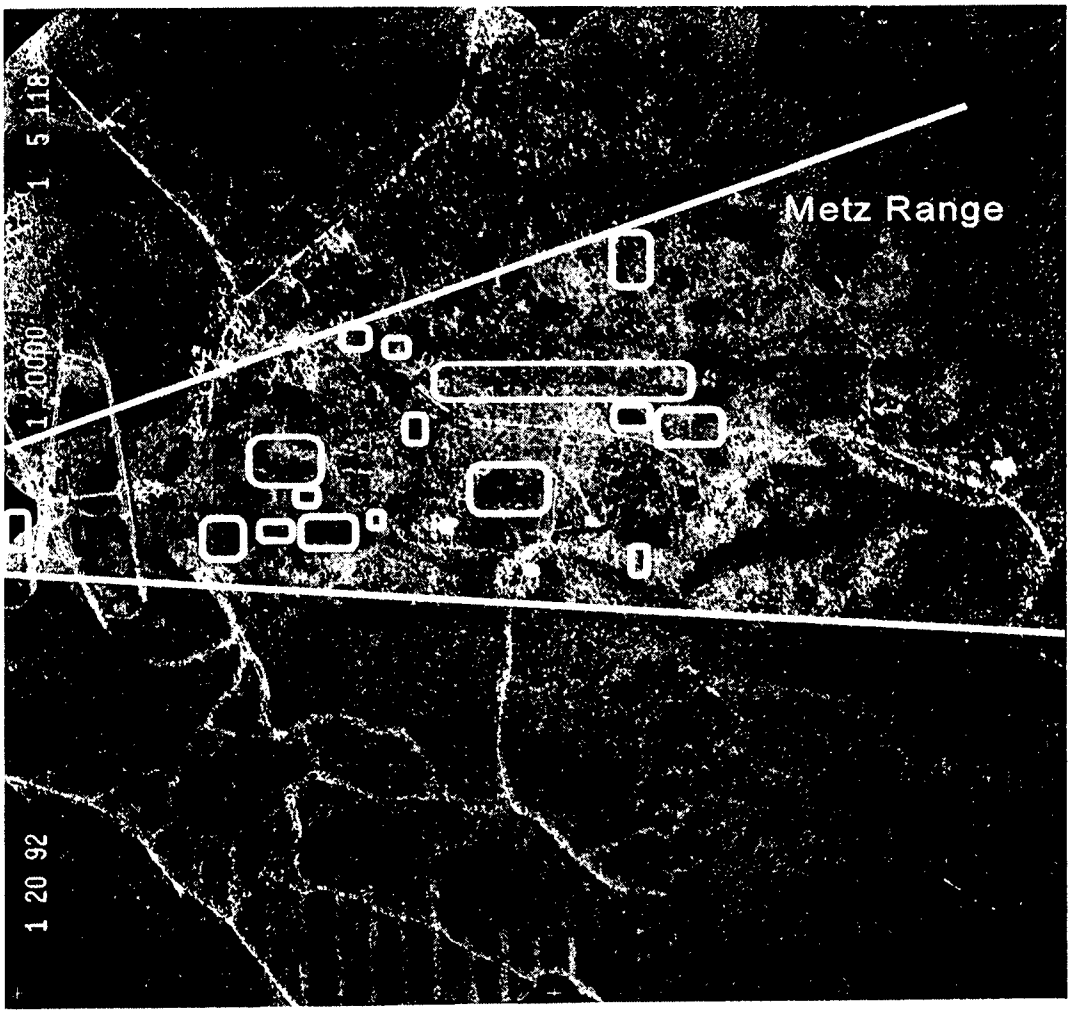


Significant vehicle disturbance through center of picture resulting in heavily disturbed vegetation and soil.

Severe vehicle disturbance in foreground of picture resulting in near complete removal of the vegetation layer and destruction of the soil surface layers.

Figure 5. *B. atropurpurea* habitat heavily impacted by military ORV training and testing.

and periodic fires (Folkerts 1982). However, Folkerts believes that regardless of the moisture regime and soil conditions, absence of fire will result in the loss of bog species. Coastal Plain bogs are considered fire subclimax or disclimax communities



The dark areas outside of Metz Range are primarily pine woodlands and wooded wetlands, while the lighter areas inside Metz Range are a mix of open grassland, savanna, and wooded wetlands.

Figure 6. Aerial photograph of Metz Range in 1992 showing open conditions and approximate locations of the largest *B. atropurpurea* populations.

and depend on fire to eliminate competitors and also release nutrients bound up in the organic matter from previous growth (Eleutarius and Jones 1969; Folkerts 1982). If fire is suppressed and woody species invade, increased transpiration lowers the water level in bog soils allowing further invasion by less moisture-tolerant species. Over a 20-year period this can eliminate a typical bog community (Folkerts 1982). For example, Plummer (1963) and Pullen and Plummer (1964) report a change in the floral composition of the moist pine barrens between 1906 and 1962. They document the introduction of about 98 new species and the elimination of around 50 species with *B. atropurpurea* being one of the missing species. They cite land conversion and drainage as the cause of the change in species composition.

The burn history for each of the *B. atropurpurea* populations at Fort Stewart is presented in Appendix A. This information is based on GIS data delineating the areas of Fort Stewart burned in the summer and winter of each year since 1990. The exact timing and uniformity of the burns over these areas is unknown. Consequently, the actual burn history for each population remains questionable. It is possible that all of the populations have burned at least once since 1990. Winter burns appear to have been more common, however, populations 2a, 2e, 6, and n14 may have also received summer burns after 1993.

A biological inventory of Fort Stewart was completed in October 1994 (TNC 1995a). In this effort six *B. atropurpurea* populations were discovered (Georgia Natural Heritage Program (GNHP) Element of Occurrence (EO) numbers 701-706). An additional inventory specifically for *B. atropurpurea* was conducted in the late summer of 1995 and documented an additional 14 populations (Helton in prep). These inventories set the stage for this project.

A basic understanding of the biology and ecology of a species is necessary to generate management plans, demographic studies, and hypotheses which may be tested through experimentation and lead to improvement in conservation strategies. The principal research question and specific task area questions (population data, vegetative growth, reproduction, phenology, environmental data, and discriminant analysis) addressed in this study are presented in Table 1. These questions have not been studied for *B. atropurpurea* at Fort Stewart or elsewhere. This is believed to be the first quantitative study on the ecology of this species.

This study characterized the condition of the *B. atropurpurea* populations at Fort Stewart as the next contribution to the TES conservation management framework. Knowledge of the number and location of populations for species of concern is important for natural resource managers at Fort Stewart. Without this information they cannot begin to solve possible conflicts between military training and testing and natural resource conservation, and among natural resource management activities themselves. Knowledge of the number of individuals present in each population is also beneficial. The number of individuals present in a population has an influence on population persistence and is a key factor in determining management prescriptions to apply to each population. Moreover, the spatial arrangement of flowering individuals and populations may have a significant influence on pollinator activity (Handel 1983 and references therein; Jennersten 1988; Murawski and Hamrick 1991; Widen 1993; Agren 1996) and consequently population persistence. The vegetative condition of a population is often a preliminary indicator of the relative health of the individuals. It also sheds light on the possible limiting factors of population persistence since many life-history events are size

dependent (Harper 1977; Kirkpatrick 1984; Menges 1991 and references therein). Similarly, reproduction is an important aspect of the life-history of plants. The reproductive status of a population is often a key indicator of the likelihood for persistence. It also sheds light on the possible limiting factors of population persistence. An understanding of the breeding system, dispersal mechanisms, and overall reproductive success is a necessity to develop management plans. Environmental conditions often have a significant influence on population persistence. Most life-history events, particularly germination, growth, reproduction, and dispersal require specific environmental conditions in order to succeed. Hydrology, light level, and disturbance have been identified as important environmental parameters that may affect the reproduction and health of *B. atropurpurea* (Smith 1994; TNC 1995b). An initial assessment of *B. atropurpurea*'s population sizes and structure, vegetative condition, reproductive capacity, and environmental condition of each population (habitat quality) was necessary to provide a baseline or reference point for future studies and to begin to understand the basic biology of this species. Moreover, it was necessary to identify characters that may indicate change in vegetative or reproductive vigor and attributes that may indicate change in population structure or quality. This information was needed to plan the design of a demographic study, generate hypotheses to be tested in more rigorous experimental studies, and aid the prioritization of populations for conservation.

In natural resource management, difficult decisions have to be made on how to best use the available resources to conserve a species of concern. Often there are not enough resources available to protect every population of a species. Under such circumstances priority must be given to the protection of certain populations while others receive a lower degree of protection. The selection of such populations often rests on assessments of the population genetic or ecotypic uniqueness, site quality, and the degree of threat to population persistence. A preliminary genetic study on *B. atropurpurea* at Fort Stewart revealed little genetic differentiation (Halward, Hill, and Shaw in prep). Consequently, an initial assessment of the degree of separation among the populations based on the vegetative and reproductive characters using descriptive discriminant analysis was necessary to provide a baseline or reference point for future studies and to begin to understand the basic biology of this species. Moreover, it was necessary to examine the possibility of local ecotypes and identify unique populations in order to aid prioritization of populations for conservation, plan the design of a demographic study, and generate hypotheses that can be tested in more rigorous experimental studies.

3 Materials and Methods

Field Sampling Design and Methods

Fieldwork for both the 1995 and 1996 growing seasons was originally planned for a 6-week period from mid-August through September. However, delayed access to the Fort Stewart training areas did not permit fieldwork to begin until early September in 1995. During August 1995, several visits were made to *B. atropurpurea* populations outside of Fort Stewart (GNHP Element of Occurrence [EOs] 9, 33, and 40) to examine the habitat and test different sampling and mapping strategies. In both years, approximately half of the field time was spent conducting searches to locate and determine the boundaries of the known *B. atropurpurea* populations; the remaining time was spent sampling the populations. See Table 2 for a summary of sampling and statistical procedures for each project task area in 1995 and 1996.

The extent of each population was verified by ground survey and the boundary delineated. The word 'population' does not refer to a population in the genetic sense, but refers only to a distinct physical occurrence of the species within the landscape (a study site). In 1995, five of the six known populations were sampled (GNHP EOs 701 - 704, and 706). Population six (EO 705) was not found. The population delineations followed those made by TNC. Due to the shortened sampling time in 1995, the sampling was biased by selecting only the areas where *B. atropurpurea* was most abundant (highest densities) (Figure 7). This bias may have resulted in sampling larger, healthier individuals in the higher quality habitat. In 1996, 27 populations were sampled, including all 6 previously known populations and the 14 additional populations discovered in 1995. The apparent increase from 20 populations to 27 populations in this study represented a more accurate delineation of the populations based on hydrologic and topographic position of the populations. Several of the populations delineated by TNC as a single EO due to their close proximity (e.g., EOs 703, 704, and 706) actually appeared to be distinct entities based on apparent hydrologic and topographic separation. These EOs became populations 3a-3f, 5a-5c, and 2a-2f, respectively. That is, the populations were separated by an area of upland that appeared to break the continuity of the wetland matrix. The re-delineation was accomplished primarily to validate the homogeneity of each sampling area. In 1996, a Trimble

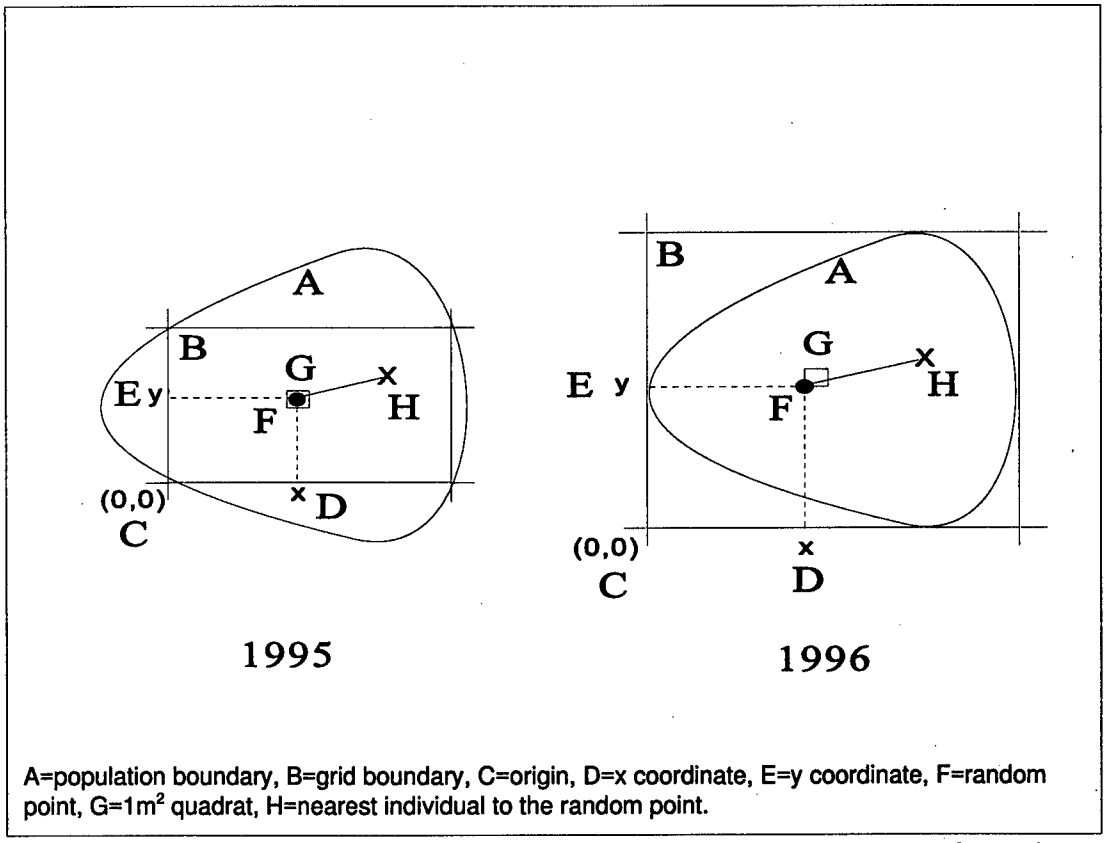
Table 2. Comparison of sampling and statistical methodologies between the 1995 and 1996 project tasks.

Project Task Area	Task Area Subunit	1995	1996
Overall Sampling	Sampling Unit	Grid Areas Within Population	Grid Area Around Population
	Sampling Method	Random (x,y) Coordinates	Random (x,y) Coordinates
	Quadrats	Centered Around Individual	Placed at Random Point
	Individuals	Nearest Individual	Nearest Individual
Population Data	Map	---	GPS and GIS Data
	Population Size	---	Density x Area
	Density	Per Quadrat	Per Quadrat
	Dispersion	---	Quadrats and Distance Measures
	Statistics	Descriptive	Nonparametric ANOVA and Descriptive
Vegetative Data	Ramets	Per Genet	Per Genet
	Stems	Per Genet	Per Genet
	Stem Height	Per Ramet	Per Genet
	Basal Leaves	Per Ramet	---
	Inflorescences	Per Ramet and Genet	Per Genet
	Statistics	Descriptive	Descriptive
Reproduction Data	Inflorescence Density	Per Quadrat	Per Quadrat
	Capitulum Width	Per Inflorescence	---*
	Ray Flowers	Per Inflorescence	---
	Seed Count	Per Inflorescence	---
	Seed Set	Per Inflorescence	---
	Seed Mass	Per Inflorescence	---
	Seedling Emergence	Per Inflorescence	---
	Emergence Rate	Per Inflorescence	---
	Statistics	Wilcoxon and Descriptive	Nonparametric ANOVA and Descriptive
Phenology	Vegetative and Reproductive	Field Observations	Field Observations
Environmental Data	Disturbance Type	---	Per Quadrat
	Disturbance Degree	---	Per Quadrat
	Light Level	---	Per Quadrat
	Statistics	---	Chi-square, Nonparametric ANOVA, and Descriptive
Discriminant Analysis	Principal Components Analysis	---	Vegetative and Reproductive Variables
	Manova	---	Vegetative and Reproductive Variables
	Canonical Discriminant Analysis	---	Vegetative and Reproductive Variables

* Indicates no sampling data collected during the sampling year.

Pathfinder™ GPS unit (Trimble Navigation Ltd., Sunnyvale, CA 94086) using an MC-V® Data Collector (Corvallis MicroTechnology, Inc. Corvallis, OR 97333) with Asset Surveyor™ software v. 2.50 (Trimble Navigation, Ltd.) and Pfinder™ software v. 2.53 (Trimble Navigation, Ltd.) was used to delineate the boundary of each population. This position data was then input in the Geographic Resources Analysis Support System (GRASS) GIS v. 4.1 (USACERL, Champaign, IL 61821) where population maps were produced and the population areas calculated. Then, a grid based on the dimensions of each population was superimposed over the entire population for sampling (Figure 7). For large or irregular-shaped populations multiple adjacent grids were used while keeping the x-axis contiguous.

Sampling was conducted in a hierarchical fashion. First, a training area was selected using random selection without replacement. Second, a population within that training area was selected using random selection without replacement. Third, random points within that population were generated. Based on the dimensions of each grid, pairs of numbers (x,y coordinates) were generated using random selection without replacement. The corner of each grid in the southwest sector (180°- 270°) served as the origin (0,0 coordinate). In 1996, there was only one origin per population. Last, the closest *B. atropurpurea* genet to each random point was



A=population boundary, B=grid boundary, C=origin, D=x coordinate, E=y coordinate, F=random point, G=1m² quadrat, H=nearest individual to the random point.

Figure 7. Schematic diagram of the sampling process involved in locating the random point 1m² quadrant, and nearest individual in 1995 and 1996.

sampled. This four-step process continued until each population had been visited. One pass through all populations was considered a round. As many rounds as possible were made during the allotted sampling period. Furthermore, because the sampling was done over a 14-day period in 1995 and a 25-day period in 1996, populations were selected at random times throughout the sampling period.

In 1995, the number of sampling points per population (sampling intensity) was proportionate to the visually estimated population size (flowering individuals). At each population at least 30 points were sampled on the first round. For the second round an additional number of points, based proportionately on the population size and depending on the time remaining to sample, were sampled for the larger populations. That is, if a population was twice as large, an additional 30 points were sampled, if time permitted. Populations encompassing a relatively large area were divided into two or more grid areas to facilitate easier sampling, but the grids were not contiguous. If multiple grids were used, the total number of sampling points was evenly distributed among all grid areas.

In 1996, a more uniform sampling intensity was attained. At each population 20 random points were located on the first round regardless of the number of flowering individuals in the population, and 15 points (depending on time remaining to sample) on each successive round for as many rounds as possible or until the population was completed (censused). Populations with fewer than 30 individuals were censused on the initial round and eliminated from further rounds to save time. Three sampling rounds were completed. As the sampling progressed the smaller populations were completed leaving only the large populations in the final rounds.

In 1995, a $1m^2$ quadrat was centered around the random sample genet (described below) and oriented with the cardinal directions. The quadrat was the unit of measure for estimating genet and floral density. This procedure provided an inflated estimate of density; however, preliminary information on the spatial distribution of individuals and adequacy of the quadrat size was obtainable (Figure 7). In 1996, a $1m^2$ quadrat was situated perpendicular to the grid sides at each random sample point with the lower left corner on the point. The quadrat was the unit of measure for estimating the genet and floral density, population sizes, dispersion of individuals, and environmental characterization of the populations (Figure 7). An estimate of population size was calculated from the density estimates and the calculated area of each population (density times area equals population size). In several populations none of the quadrats recorded "hits" of *B. atropurpurea* individuals within the quadrat even though individuals were present. Consequently, the density estimate was zero; which would obviously underestimate the number of individuals present in the population. Therefore, an alternate method

was used to estimate density in these populations. Based on random point-to-nearest-individual distances (described below) a closest individual (CI) calculated density can be computed. However, this method assumes a random distribution of the individuals and this was believed to be unlikely. Consequently, these density estimates were biased in the more conservative direction. See Bonham (1989) for computational procedures and details.

In 1995 and 1996, at each random sample point the nearest *B. atropurpurea* genet (a single cluster of stems/rosettes) was identified as the random sample individual. The distance from the sample point to the nearest individual was measured (cm) and the individual's azimuth was recorded. This information helped relocate individuals for seed collection and provided an alternate method for examining the density and dispersion of individuals within the population (Figure 7). The sample genet (and ramet in 1995) was the unit of measure for estimating the vegetative and reproductive condition of the populations. The number of ramets (single rosettes/stems within cluster) and stems was counted for each genet. In 1995, one stemmed ramet, in the most developed stage, was selected for more intensive measurements to characterize mature, reproductive individuals. If more than one ramet existed in the same developmental stage, one was randomly selected. The ramet's stem height was measured (cm) from the ground surface to the base of the highest capitulum and the number of inflorescences was counted. Two leaves were selected (if present) and the length (cm) and width (cm) at the longest and widest point were measured. The number of basal leaves ranged from none to greater than ten, therefore, no random process was involved in selecting the leaves, since there was often no choice. The average of the measurements of the two leaves (if available) was used to characterize basal leaf growth for each ramet. In the preliminary sampling it was determined to be too time consuming to count the number of basal leaves per ramet. In 1996, the sampling methodology was improved based on results of the 1995 sampling. *B. atropurpurea* individuals tended to exist as single ramets or as clusters of ramets. Examination of the underground structure of a few clusters revealed rootstock connections among the ramets; therefore, many of the clusters were probably single genetic individuals. Consequently, the genet was chosen as the unit of measurement for the vegetative characters assuming the rosettes were connected. Furthermore, a decision was made to measure the height of all stems within the genet and use the average stem height to characterize the genet. This would eliminate any bias in selecting a ramet to sample. Also, the number of inflorescences was counted on all stems within the genet. It was determined that the basal leaf measurements were probably not useful in characterizing the ramets or genets since mature ramets tend to lose many of the leaves during anthesis. The number of ramets, stems, and inflorescences per genet

was counted. The height (cm) of all stemmed ramets per genet was measured and the average stem height recorded. Stem height was measured as described above.

In 1996, three indices of dispersion were calculated and compared to examine the pattern of individuals within each population. The Coefficient of Dispersion or Variance-to-Mean Ratio (I) and the Standardized Morisita's Index of Dispersion (I_P) are based on quadrat counts of individuals. Eberhardt's Index of Dispersion (I_E) is based on random point-to-nearest-individual distances. The coefficient of dispersion is one of the oldest and best measures of dispersion; however, it may become problematic when applied to clumped populations. The standardized Morisita's index is placed on an absolute scale from -1.0 to +1.0 with 95% confidence limits at -0.5 and +0.5, making it more easily interpretable. This index is considered to be the most reliable since it is independent of population density and sample size. Nonetheless, these two indices have computational problems when zeros (zero density) are entered into the formulas. Eberhardt's index is a satisfactory index that does not depend on the density of the population. It also avoids the zero density computational problems. See Krebs (1989) for computational procedures and details.

In 1995, inflorescences in the most developed stage on the randomly selected ramet were selected for more intensive floral and seed measurements. If more than one inflorescence per ramet existed in the same developmental stage, one was randomly selected. The number of ray flowers was recorded and the diameter (cm) of the capitulum was measured. If the inflorescence was mature and appeared to have completed pollination, a nylon bag was placed over the inflorescence and secured with a twist-tie. The nylon bag was used to prevent seed loss from the inflorescence because the stems and inflorescences have a tendency to droop or topple over (Ron Determann, Atlanta Botanical Garden, Horticulturalist, personal communication). An aluminum tag was then placed around the base of the ramet stem to identify the ramet. In mid-November the bagged inflorescence and an unbagged control inflorescence from the same ramet were collected from each sample individual and shipped to the University of Illinois for processing. The paired sample was collected to check if the bag had any effect on the development of the seeds. The number and fresh mass of all seeds per inflorescence was recorded. Seed collection followed the guidelines established by the Plant Conservation Roundtable (of the Washington Native Plant Society) for the collection of seeds from rare plants and collection permit #95002 obtained from the Georgia Department of Natural Resources Protected Plant Program. In 1996, only the number of inflorescences per genet was recorded. No floral measurements were made and no seed was collected, since the 1995 viability study produced usable results. This eliminated any additional negative impact on the reproductive potential of the species and followed the Plant

Conservation Roundtable guidelines. Vegetative reproduction was examined on a few individuals by excavating the root system. One voucher specimen was collected; all other plants were replanted.

In January 1996, the seeds were sent to Ron Determann at the Atlanta Botanical Garden for viability testing because he had successfully germinated seeds in the past (Smith 1994; TNC 1995b; Ron Determann personal communication). He used a 4-week moist, cold stratification at 6 °C - 9 °C. The cooler was nearly dark with only one small incandescent bulb. The seeds from each inflorescence comprised a sample and were sown into a 3-inch plastic pot. The seeds were sown onto a moistened 5:1:1 mixture of peat, sand, and "Nodampoff"™ milled horticultural sphagnum moss (Mosser Lee Co., Millston, WI 54643) topped with a sprinkle of milled sphagnum.* An additional sprinkle of milled sphagnum was added on top of the seeds before being watered. The pots were then placed onto two germination carts with an 18-hour light regime. After 9 days a timer broke and these pots were exposed to a 24-hour light regime. Based on his past work with *B. atropurpurea*, Mr. Determann believes that the seeds may require light to germinate, and definitely require the cold, moist stratification. When mold was visible on any of the seedlings they were treated with Domain® fungicide (Thiophanate Methyl 46.2%) (Grace Sierra Crop Production Co., Milpitas, CA 95035).* If the seedlings were growing out of the soil, the radicles were pushed back into the soil and watered to ensure survival. Each day the number of emerged seedlings present and the number of nonviables (seedlings lacking chlorophyl) present was recorded. Nonviables were counted separately because they will not survive to become seedlings. The recording of seedling emergence in the greenhouse was stopped on day 14 because germination was believed to be at least 95% complete. On day 15 the samples were fertilized with Stern's Miracid® 30:10:10 fertilizer (Stern's Miracle Grow Products Inc., Port Washington, NY 11050) because the pale leaves indicated starvation. The mature plant material was used for other conservation purposes at the Atlanta Botanical Garden, and by T. Halward at Colorado State University for genetic variation testing.

In 1995 and 1996, at each visit throughout the year notes were taken on the developmental stage of *B. atropurpurea*. Seedling emergence, rosette growth, stem elongation, flowering, seed dispersal, and winter dormancy were the recognized life-history/growth stages. An attempt was made to capture the beginning (first observance), peak (>50% observance) and completion (last observance) of these events. A phenological time line for each event was then constructed. However, due to logistical problems this was only an attempt to help clarify the current under-

* Citation of trade names does not constitute an official endorsement nor approval of the use of such commercial products by the U.S. Army or the Department of Defense.

standing of this species' phenology. Discussions with other professionals acquainted with *B. atropurpurea* were also used to help fill in the phenological gaps.

In 1996, qualitative notes on the condition of each quadrat, in terms of disturbance and light level, were recorded. Disturbance type was categorized as natural (N) or human (H), and disturbance degree as low (1), medium (2), or high (3). Natural disturbance primarily referred to fire, animal disturbance, and other natural events. Human disturbance primarily referred to military ORV traffic, RCW cavity tree management, road maintenance, bivouac sites, foot traffic, extractive land uses, and other human activities. Low disturbance degree was characterized by little or no physical signs of alteration, moderate disturbance degree by some physical signs of alteration but not too severe, and high disturbance degree by severe physical signs of alteration to the soil or vegetation. Light level was categorized as low (shaded; 1), moderate (part sun; 2), or high (full sun; 3). Low light level was characterized by a significant degree of shading, moderate light level by some degree of shading but not too significant, and high light level by little or no shading at or near the ground surface.

Statistical Analyses

General descriptive statistics were calculated for all quantitative data. Exploratory data analysis was performed to check normality and other assumptions for inferential statistical analyses. All statistical analyses were performed on the raw data and where necessary, nonparametric analyses were used to test for differences among the independent class variables (environmental classes or populations) based on the dependent variables (vegetative and reproductive characters). Frequency distributions were used to characterize and test relationships among the qualitative environmental variables. All analyses were performed using the SAS® System version 6.11 (SAS Institute Inc., Cary, NC 27513) software package and Microsoft® Excel version 5.0 (Microsoft Corporation, Redmond, WA 98052). Methods are presented in detail below, for each of the project tasks. See Table 2 for a summary of sampling and statistical procedures for each project task area in 1995 and 1996.

In 1995, descriptive statistics were calculated for the density, vegetative, and reproductive measures. The density, vegetative, and reproductive measures were pooled from the within population grid areas to calculate the descriptive statistics for each population. To provide an overall characterization on Fort Stewart, the density, vegetative, and reproductive measures were pooled across populations to calculate separate overall means. The results for the 1995 fieldwork are presented

in Appendix D, except for the floral and seed data that are presented in the **Reproduction** section of Chapter 4.

In 1995, a Wilcoxon signed rank test (nonparametric paired t test) was performed on the paired seed samples to test for a significant difference between the bagged and unbagged control samples for total ovule number, mature seed number, seed set, total seed mass, individual mature seed mass, and proportion seedling emergence. This was done to check if the bag had any effect on the development of the seeds. Because of the small sample sizes within populations, no additional inferential statistics were performed.

In 1996, descriptive statistics were calculated for the density, vegetative, and reproductive measures for each population. To provide an overall characterization on Fort Stewart, these measures were pooled across populations to calculate overall separate means. A one-way nonparametric ANOVA was performed on the number of genets and the number of inflorescences per quadrat to test for differences among the populations, separately. Scheffé post hoc multiple comparisons were performed to identify significant differences among pairs of populations. The results for the 1996 fieldwork are presented in Chapter 4.

In 1996, the frequency distributions for the environmental condition characterizations were summarized for each population. To provide an overall summary of the environmental condition on Fort Stewart, the frequencies were pooled across populations. Separate Chi-squared (χ^2) tests for independence between disturbance type and disturbance degree, disturbance type and light level, and disturbance degree and light level were performed to test for dependency between the variables. A one-way nonparametric ANOVA was performed on the number of genets and the number of inflorescences per quadrat to test for differences among the levels of each of the environmental condition class variables, separately. Scheffé post hoc multiple comparisons were performed to identify significant differences among pairs of class levels.

Discriminant Analysis

In 1996, two analyses were used to reveal the relationship and degree of separation among the populations with respect to four vegetative and reproductive variables. Due to the exploratory nature of this study, principal components analysis (PCA) and descriptive (canonical) discriminant analysis (DDA) were chosen as the multivariate statistical techniques. See Table 2 for a summary of sampling and statistical procedures for each project task area in 1995 and 1996.

First, PCA was used to separate individuals into preliminary groups based on a group of correlated vegetative and reproductive characters (ramets per genet, stems per genet, inflorescences per genet, and stem height). The PCA was performed using the correlation matrix because the variables had different units of measurement. If each population had unique ecotypic variation, preliminary groups were expected to parallel the original population delineations. The eigenvalues of the PCA identified the uncorrelated linear combinations of the variables (principal components) that explained most of the variation in the variables. The correlations between the principal components and the original variables (loadings) were used to interpret the meaning of the components. Consequently, PCA also served as a data reduction technique by identifying which of the original correlated variables would be unimportant in explaining the variation among the variables in additional statistical analyses. The first two principal components explain the most variation and were used to plot the principal component scores against each other in two-dimensional space in order to visually examine the structure among the populations. If ecotypic variation existed among the populations, they were expected to be spatially separated within the principal components space. PCA was used as an exploratory data analysis technique to examine the degree of structure in the data.

Second, DDA was used to reveal differences among the populations and to identify the variable that was responsible for the majority of the separation. Once again, if each population had unique ecotypic variation, the populations were expected to be separated in the canonical components space. The goal of DDA was to maximize the canonical correlation between the grouping variable and a linear combination of the four vegetative and reproductive (outcome) variables; in other words, to maximize the separation among the populations. The task was to find a set of weights (canonical discriminant coefficients) for the outcome variables that determined a linear combination (linear discriminant function) that maximized the separation among the populations. These coefficients were the elements of the eigenvector (raw canonical coefficients) for the linear discriminant function. There were four "r" = min ("p", "q") linear discriminant functions where, "p" = the number of outcome variables, and "q" = the number of populations - 1. These linear discriminant functions were uncorrelated and each successive function was determined so as to maximize the population separation after the preceding functions were partialed out.

The number of linear discriminant functions used to interpret the population differences was determined by a test of dimensionality using sequential multivariate analyses of variance (MANOVA) and by examining the proportion of the variance accounted for by each successive linear combination. In the test of dimensionality each succeeding Wilk's lambda (Λ) was used to test the significance of residual

effects after the effects of the preceding dimensions (linear combinations) were partialed out. In the proportion of the variance explained approach, a substantive decision was made on the point where enough of the variance had been explained by the linear discriminant functions, through assessment of their respective eigenvalues. Similarly, the first two canonical components (linear combinations) explain the most variation and were used to plot the mean canonical component scores (centroids) against each other in two-dimensional space in order to visually examine the structure (separation) among the populations. In addition, the linear discriminant function that maximized the variation among the populations was used to classify each observation based on values for the four predictor (outcome) variables to one of the populations. This was a predictive discriminant analysis (PDA). If ecotypic variation existed among the populations, observations from the same population were expected to be classified together. Posterior probabilities of population membership and error count estimates indicated how much confidence there was that the classifications were correct and how disparate the populations really were.

The meaning of the linear discriminant functions was described by examining the correlations (loadings) between the linear combination scores and the outcome variables (within population canonical structure correlations). These correlations provided a direct indication of the variables that were most strongly associated with the latent characteristic that the discriminant functions represent. These were rational interpretations of the meaning of the linear combinations.

The variable most responsible for the separation among groups was determined by conducting successive MANOVAs removing each outcome variable in turn and examining the resulting Wilk's lambda values (Λ). The variable most responsible for the separation was the one where the MANOVA on the remaining variables had the largest Λ value. The ranking of the remaining variables was conducted in the same manner based on the second, third, and fourth largest Λ values.

Finally, a MANOVA was used to test the statistical significance of population mean differences. The null hypothesis tested was the simultaneous equality of population means on the four outcome variables. Wilk's lambda was the criterion used for this statistical test. An inverse relationship exists between the Λ value and the degree of separation among the populations. Tau squared was also used as an index of the strength of association ($\tau^2 = 1 - \Lambda^{1/r}$). Statistical tests were also performed on all possible pairwise comparisons between the populations to determine the populations that were significantly separated from each other. All analyses were performed using SAS® version 6.11 CANDISC, DISCRIM, GLM, and PRINCOMP procedures. See Stevens (1996) and Huberty (1994) for details on discriminant analysis methods.

4 Results and Discussion

Due to the logistical and sampling difficulties encountered in 1995, much of that data has been treated as preliminary exploratory information and is presented in Appendix D. No statistical analyses were performed due to the small sample sizes and bias in the data. The data did provide preliminary information, particularly with respect to the seed data. In addition, the discovery of 14 new populations in 1995 required the expansion of the sampling and characterization in 1996. Consequently, the 1996 data can be viewed as the true baseline of information characterizing the condition of *B. atropurpurea* at Fort Stewart, except for the 1995 seed data. A more extensive treatment of the 1995 data and 1996 data can be found in Lincicome (1998).

Population Data

Population Size

The number of *B. atropurpurea* populations and the number of individuals occurring on Fort Stewart were much greater than initially assumed. It is now highly probable that Fort Stewart contains the greatest number of known populations and individuals of this species in the Southeastern United States. The word 'population' does not refer to a population in the genetic sense, but refers only to a distinct physical occurrence of the species within the landscape (a study site). As noted earlier, six populations were documented by TNC through 1994, an additional 14 populations were documented by C. Helton in 1995, and currently, 29 populations have been delineated. The current number of populations includes the one additional population discovered in 1996 that was not included in this study. It should also be noted that population n3, discovered by C. Helton in 1995, was not found again in 1996 and was not included in this study. This was a small population of only nine flowering individuals (Helton in prep). This population had been significantly disturbed by military ORV traffic, which may have eliminated these individuals. The apparent increase from 20 populations to 27 populations in this study represented a more accurate delineation of the populations based on hydrologic and topographic position of the populations. Several of the populations delineated by TNC as a single EO due to their close proximity (e.g., EOs 703, 704,

and 706) actually appeared to be distinct entities based on apparent hydrologic and topographic separation. These EOs became populations 3a-3f, 5a-5c, and 2a-2f, respectively. That is, the populations were separated by an area of upland which appeared to break the continuity of the wetland matrix. The re-delineation was accomplished primarily to validate the homogeneity of each sampling area. Despite this decision, management of populations in close proximity should not treat the populations in isolation but as one landscape unit.

In 1996, population areas and mean quadrat densities yielded a total estimated population size of 44,299 flowering and nonflowering genets on Fort Stewart (A x B = Population Size, Table 3). However, in populations 2f, n2, n5, n7, and n11, none of the sampled quadrats contained *B. atropurpurea* genets; therefore, an estimated mean density of 0 genets/m^2 was obtained. Consequently, point-to-nearest plant distance was used to yield a closest individual (CI) calculated density estimate. Density estimates based on the CI method have low accuracy and are biased for species showing aggregation by underestimating the true density (Bonham 1989). Furthermore, the CI density estimates were based only on flowering individuals and not those individuals remaining in the rosette stage. Therefore, these estimates should be viewed as a conservative estimate of density. Nonetheless, for comparison, the use of the CI calculated density yielded an estimate of 6,516 flowering genets on Fort Stewart. Many of the estimated population sizes based on the CI calculated density were reasonably close to the number of flowering genets actually censused per population (Table 3). Since these estimates were based only on flowering individuals one additional correction was made. The population size estimates based on the CI calculated density or the number of flowering genets censused per population and the proportion of flowering genets in 1995 yielded a corrected population size of 10,477 flowering genets (C or D / 0.609 = Corrected Population Size, Table 3). If the population was censused, that number of flowering genets was used in the corrected calculation rather than the CI estimated number of flowering genets. Since the CI calculated density was based only on the flowering genets, this correction adjusted the estimated population size to account for the proportion of the population that was nonflowering. Since weather conditions were similar in 1995 and 1996 and the proportion of flowering ramets was similar in both years (60% and 56%, respectively), the above correction was made under the assumption that the proportion of flowering genets in 1996 would have been similar to the 61% in 1995 (the proportion of flowering genets was not determined in 1996). Consequently, this correction was made only to help improve the lower bound population size estimate. Based on personal observations in the field, these corrected population size estimates appeared more reasonable than the population size estimates based only on the CI calculated density. However, because the corrected population size estimates still rely on the CI calculated density estimates,

Table 3. Population size characteristics.

Population	Area (m^2) (A)	N	Proportion Area Sampled by Quadrats	Quadrat Density ($1m^2$) (B)*	Quadrat Estimated Number of Genets	CI Calculated Density (C)	CI Estimated Number of Genets	Number of Flowering Genets Censused (D)	CI Corrected Estimated Number of Genets
1	2,202	50	0.0227	0.44	969	0.09	198	----*	325
2a	80,032	50	0.0006	0.04	3,201	0.02	1,601	----	2,628
2e	11,763	50	0.0043	0.16	1,882	0.03	353	----	579
2f	8,799	21	0.0024	0.00	0	0.01	88	21	34
3a	4,705	50	0.0106	0.20	941	0.06	282	----	464
3b	1,398	50	0.0358	0.58	811	0.12	168	----	275
3c	17,359	50	0.0029	0.24	4,166	0.02	347	----	570
3d	39,265	50	0.0013	0.36	14,135	0.03	1,178	----	1,934
3f	1,144	40	0.0350	0.25	286	0.03	34	40	66
4	1,701	50	0.0294	0.38	647	0.04	68	----	112
5a	96	12	0.1250	0.67	64	0.11	11	12	20
5b	1,276	44	0.0345	0.34	434	0.04	51	44	72
5c	1,135	26	0.0229	0.19	216	0.03	34	26	43
6	255	18	0.0706	2.00	511	0.07	18	18	30
n1	206	19	0.0922	0.05	10	0.03	6	19	31
n2	4,474	46	0.0103	0.00	0	0.02	89	46	76
n4	219	44	0.2009	0.36	79	0.04	9	44	72
n5	1,373	10	0.0073	0.00	0	0.02	27	10	16
n6	45,736	50	0.0011	0.06	2,744	0.02	915	----	1,502
n7	79	1	0.0127	0.00	0	0.00	0	1**	3
n8	2,616	12	0.0046	0.08	209	0.02	52	12	20
n9	3,201	47	0.0147	0.02	64	0.01	32	47	77
n10	1,279	40	0.0313	0.25	320	0.03	38	40	66
n11	6,489	51	0.0079	0.00	0	0.01	65	51	84
n12	18,982	50	0.0026	0.56	10,630	0.04	759	----	1,247
n13	1,850	50	0.0270	0.94	1,740	0.03	56	----	91
n14	1,209	25	0.0207	0.20	242	0.03	36	25	41
Overall	258,85	1006	0.0039	-	44,299	-	6,516	-	10,477

* Sampled populations N=50, the Corrected Estimate assumes an average 61% of genets flowering per site in 1995.
**Three total genets were observed in this population.

the corrected population size estimates are still considered conservative. Population size estimates based on the quadrat densities were possibly excessive for some populations based on comparisons with the number of genets actually documented in the censused populations (3f, 5a, 5b, 5c, 6, n8, n10, and n14). Consequently, the two population size estimates are provided as a range; the true population size is somewhere between 10,477 and 44,299 genets.

Based on the GRASS GIS database created from the GPS survey data for each population, the 27 *B. atropurpurea* populations studied on Fort Stewart encompassed a scattered area of 258,858 m^2 (25.9 ha) (Table 3). The populations ranged from 79 m^2 (0.008 ha, population n7) to 80,032 m^2 (8 ha, population 2a). Only six populations were greater than 10,000 m^2 (1 ha) in size. Nonetheless, relative to many rare species these represented significantly large populations in terms of habitat area and number of individuals (Sawyer and Andre 1990; Boyd and Hilton 1994; Schemske et al. 1994; Drew and Clebsch 1995; Thomas and Carey 1996).

Density

The genet density estimates were difficult to accurately obtain for this species. In 1996, the overall estimated density of genets per quadrat was 0.30 genets/m^2. In comparison, the CI calculated density was 0.03 genets/m^2 (Table 4). These density estimates were relatively low as expected for most rare plants (Given 1994) and were comparable to those estimated for other rare plants (e.g., DaVilla et al. 1987; Sawyer and Andre 1990; Drew and Clebsch 1995; Kephart and Paladino 1997). The problems associated with estimating density for this species, and the differences between the quadrat and CI methods were discussed above. One probable contributing factor to the low density estimates was insufficient sample size, as shown by the proportion of the population area sampled (Table 3). This may be particularly true with respect to the aggregated distribution of this species (see more in **Dispersion** below). For instance, the large number of quadrats representing "misses" (overall only 10% of the quadrats contained genets) indicated that more sampling quadrats were needed to more accurately estimate density for this species.

Table 4. Mean (±SE) number of genets per quadrat (1m^2) and closest individual (CI) calculated density in 1996.

	N	Mean ± SE	Range
1996 Number of Genets per Quadrat	1006	0.30 ± 0.04	0 - 13
1996 CI Calculated Genet Density	1006	0.03 ± 0.00	0.00 - 0.12

Estimated mean quadrat densities per population ranged from 0.00 genets/m^2 (populations 2f, n2, n5, n7, and n11) to 2.00 genets/m^2 (population 6). In comparison, the CI calculated densities per population ranged from 0.00 genets/m^2 (population n7) to 0.12 genets/m^2 (population 3b) (Table 3 and Figure 8). Populations 6 and n13 had a high degree of variation in the number of genets per quadrat, and populations 5a and 6 had a high degree of variation in the CI calculated density as shown by the wide standard errors (Figure 8). This was most likely the result of quadrats containing very few or very many genets because the observed dispersion of individuals in these populations was very patchy. The results for a one-way nonparametric ANOVA on the number of genets per quadrat revealed a significant difference between at least two populations (F=3.47, p=0.0001) (Table 5). However, none of the Scheffé post hoc multiple comparisons were significant. Improvements

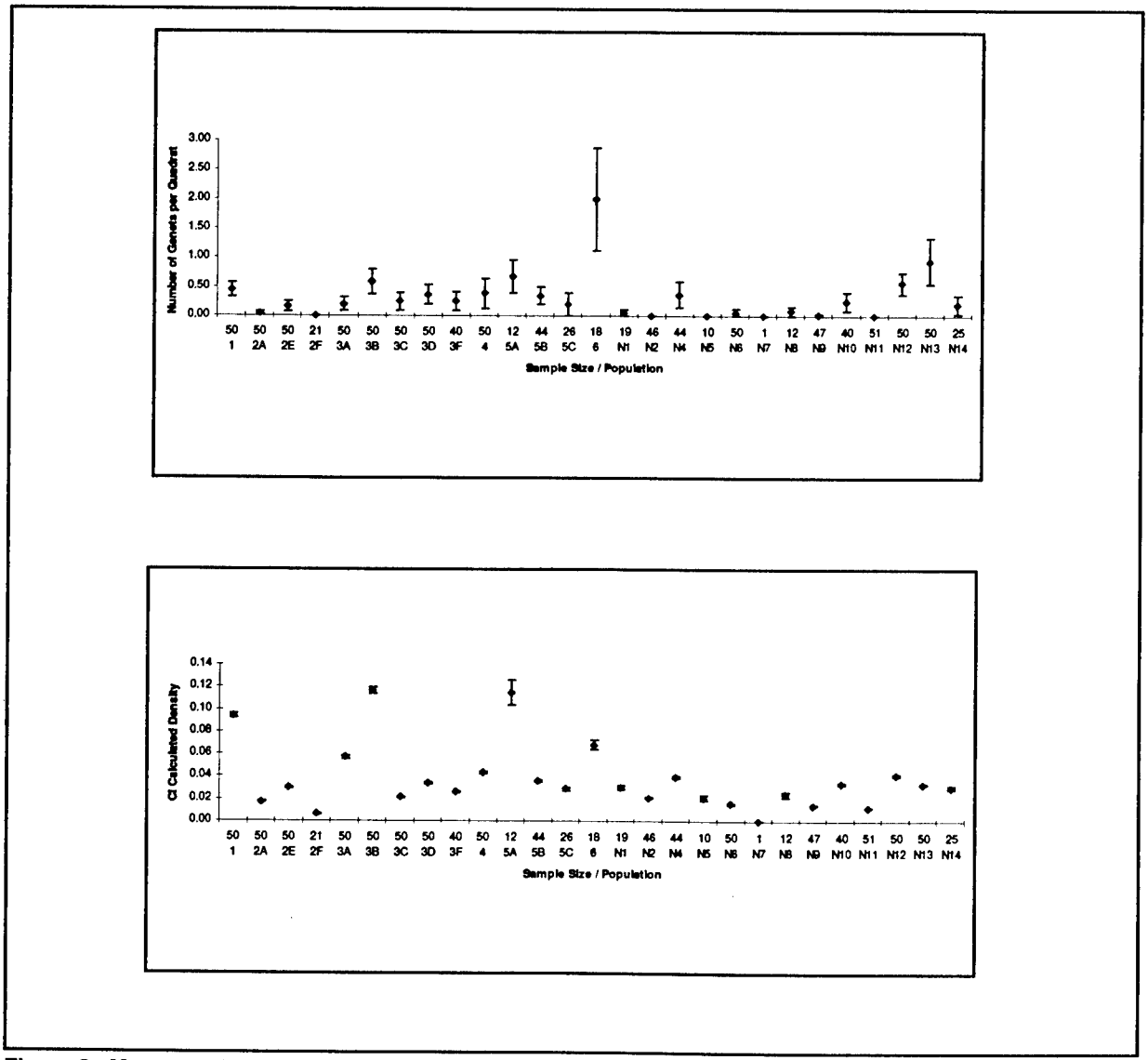


Figure 8. Mean number of genets per quadrat per population and closest individual calculated density per population in 1996.

in the sampling strategy, technique, and/or quadrat characteristics may be required to improve density estimates for this species.

Dispersion

In 1996, three measures of plant dispersion were calculated: two based on the $1m^2$ quadrat densities and one based on point-to-plant distances. The results of all three indices were in close agreement. In general, the pattern of genet dispersion was aggregated, but variable among populations (Table 6). This was consistent with results for most plant species (e.g., Kershaw and Looney 1985; DaVilla et al. 1987, Causton 1988; Bonham 1989; Menges 1991; Kent and Coker 1992; Schemske et al. 1994 and references therein).

The standardized Morisita's index (I_p) produces values that are directly comparable between -1.0 and 1.0 (<0 = regular, 0 = random, >0 = aggregated). The 95% confidence limits for the index are -0.5 to 0.5. Index values ranged from -0.03 (regular) to 1.0 (aggregated), with 18 populations showing significant aggregation (α=0.05). Populations 5a and 2a had values not significantly different from random (Table 6).

The coefficient of dispersion or variance to mean ratio (I) had similar results (<1 = regular, 1 = random, >1 = aggregated). However, in addition to populations 2a and 5a, populations n1, n8, and n9 were also not significantly different from random (α=0.05) (Table 6). The degree of dispersion for these last three populations was not able to be calculated via the standardized Morisita's index. The standardized Morisita's index had computational problems (division by zero) with populations n1, n8, and n9 because only one quadrat contained a single genet in each population. Moreover, the standardized Morisita's index and coefficient of dispersion index for populations 2f, n2, n5, n7, and n11 were not able to be calculated because the random quadrats contained no *B. atropurpurea* genets. Once again, these computational problems indicated that more sampling quadrats were probably needed to more accurately estimate density for this species.

Eberhardt's index of dispersion (I_E) also had similar results (<1.27 = regular, 1.27 = random, >1.27 = aggregated). Twenty-two populations showed significant aggregation (α=0.05). Populations 3f, 4, 5a, n9, and n10 were not significantly different from random. Population n7 was regular based on this index, but only had one observation (Table 6).

As discussed before, the standardized Morisita's index and coefficient of dispersion were both influenced by the apparent inadequacy of the quadrat method to estimate

density. In fact, only 10% of the quadrats actually contained *B. atropurpurea* genets overall. Furthermore, the coefficient of dispersion was influenced by the density of each population (Krebs 1989). Consequently, more confidence may be placed with the determination of dispersion using Eberhardt's index. Population 5a was shown to be not significantly different from random by all three measures. Population 2a, although shown to be not significantly different from random by the first two indices, was shown to be aggregated by Eberhardt's index. Populations n1, n8, and n9 were shown to be random based on the coefficient of dispersion but aggregated by Eberhardt's index. Populations 4, 3f, and n10 were shown to be aggregated by the first two indices, but not significantly different from random by Eberhardt's index. Nonetheless, the three index values empirically suggest aggregation. Based on field observations, individuals of this species tended to be clustered in patches within populations with scattered individuals between the patches.

The patchiness observed in the distribution of this species may be the result of limited dispersal distances or of variability in the suitability of patches (biotic and abiotic) to support plant establishment (Harper 1977). Seed dispersers and dispersal distances are unknown for this species. Variability in the suitability of patches to support plants may be due to natural or human causes. Patches may naturally vary in light, nutrients, and water availability, as well as, predators, pathogens, and competitors (Schupp 1995 and references therein). Human activities, such as prescribed burning and military ORV disturbances, may influence the suitability of these patches by altering the availability of resources or dynamics of predator and competitor populations. Altered distributions of individuals within populations have been observed on Fort Stewart due to military ORV disturbance. Disturbances, such as fire and ORV traffic, create a dynamic mosaic of suitable and unsuitable patches within the landscape. Because *B. atropurpurea* appears to be a disturbance dependent species (primarily fire), metapopulation structure may be important in determining its persistence in a variable environment. Human activity may also serve as a seed dispersal agent. Whatever the cause of the spatial distribution of individuals within populations, the spatial arrangement of flowering individuals and populations may have a significant influence on pollinator activity (Handel 1983 and references therein;

Table 5. One-way nonparametric ANOVA comparisons of the vegetative and reproductive variables among populations in 1996.

Variable	F	Numerator DF	Denominator DF	P	N
Genets per Quadrat	3.5	25	979	0.0001	1005
Inflorescences per Quadrat	1.6	25	979	0.0231	1005

Table 6. 1996 calculated standardized Morisita's index of dispersion, coefficient of dispersion, and Eberhardt's index of dispersion based on sampled genets per population and overall (significance level α=0.05).

Standardized Morista's Index of•				Coefficient of Dispersion				Eberhardt's Index of Dispersion			
Population	I_p	Dispersion	Significant	Population	I	Dispersion	Significant	Population	I_E	Dispersion	Significant
2f	----	--------	----	2f	----	--------	----	overall	2.29	aggregated	yes
n1	----	--------	----	n2	----	--------	----	3d	2.27	aggregated	yes
n2	----	--------	----	n5	----	--------	----	3b	2.13	aggregated	yes
n5	----	--------	----	n7	----	--------	----	n13	2.01	aggregated	yes
n7	----	--------	----	n11	----	--------	----	n8	2.00	aggregated	yes
n8	----	--------	----	n13	8.66	aggregated	yes	n12	1.95	aggregated	yes
n9	----	--------	----	4	8.15	aggregated	yes	3c	1.90	aggregated	yes
n11	----	--------	----	6	6.94	aggregated	yes	n6	1.83	aggregated	yes
5c	1.00	aggregated	yes	n4	5.77	aggregated	yes	3a	1.78	aggregated	yes
n6	1.00	aggregated	yes	overall	5.16	aggregated	yes	2a	1.78	aggregated	yes
n14	0.75	aggregated	yes	5c	5.00	aggregated	yes	5c	1.74	aggregated	yes
4	0.69	aggregated	yes	3c	4.69	aggregated	yes	1	1.73	aggregated	yes
3c	0.65	aggregated	yes	3f	4.05	aggregated	yes	5b	1.67	aggregated	yes
3f	0.65	aggregated	yes	n10	4.05	aggregated	yes	n5	1.65	aggregated	yes
n10	0.65	aggregated	yes	3d	3.94	aggregated	yes	n2	1.60	aggregated	yes
n4	0.65	aggregated	yes	3b	3.67	aggregated	yes	2e	1.56	aggregated	yes
3a	0.59	aggregated	yes	n14	3.33	aggregated	yes	n1	1.53	aggregated	yes
2e	0.59	aggregated	yes	n12	3.29	aggregated	yes	n11	1.52	aggregated	yes
n13	0.58	aggregated	yes	3a	3.06	aggregated	yes	2f	1.50	aggregated	yes
3d	0.58	aggregated	yes	n6	3.00	aggregated	yes	6	1.49	aggregated	yes
6	0.57	aggregated	yes	5b	2.72	aggregated	yes	n14	1.47	aggregated	yes
5b	0.55	aggregated	yes	2e	2.64	aggregated	yes	n4	1.46	aggregated	yes
3b	0.54	aggregated	yes	1	1.78	aggregated	yes	n9	1.38	aggregated	no
n12	0.53	aggregated	yes	5a	1.45	aggregated	no	4	1.38	aggregated	no
1	0.51	aggregated	yes	n1	1.00	random	no	3f	1.35	aggregated	no
overall	0.51	aggregated	yes	n8	1.00	random	no	n10	1.34	aggregated	no
5a	0.20•	aggregated	no	n9	1.00	random••••••	no	5a	1.30••	aggregated•	no
2a	-0.03	regular	no	2a	0.98	regular	no	n7	1.00	regular	yes

Jennersten 1988; Murawski and Hamrick 1991; Widen 1993; Agren 1996) and consequently population persistence (see more discussion in **Reproduction** below). Monitoring the change in plant dispersion and density in relation to such disturbances may be of value in furthering an understanding of the controlling factors of population dynamics and life-history strategy for this species.

Vegetative Growth

Overall, the vegetative condition and general health of *B. atropurpurea* individuals at Fort Stewart was not severely threatened by disease or predation. The main signs of leaf predation, predominantly on basal leaves, were small sections of missing leaf tissue and occasionally entirely consumed leaves. This was most likely caused by insects. However, small mammals and deer may also have been

responsible for some leaf consumption. Deer may have been responsible for entire stems being browsed. Resprouting was commonly observed on browsed individuals so the impact may be minimal, depending on phenology. Feral hogs may also have been responsible for damage to root systems because rooting evidence was commonly observed in these habitats. A couple of plants were observed with the soil upturned surrounding the individuals and the roots and rootstock completely exposed. Predation on floral structures was also observed by beetles, caterpillars, and grasshoppers. A possible fungus was also observed occasionally on the disk flowers of some individuals.

In 1996, the number of ramets per genet was relatively consistent among populations (Table 7). In general, genets were composed of more than one ramet. There were 3 ramets per genet on average with population means ranging from 2 ramets per genet (population n8) to 11 ramets per genet (population n7) (Figure 9A). Populations n5, n7, n9, and n14 had a relatively greater number of ramets per genet while populations n8 and n13 had relatively fewer ramets per genet than all other populations. Population n7 had only one observation that appeared to be a robust individual. No substantive meaning could be proposed for the relatively high or low means based on the characteristics of the populations.

Perennial plants often have two components to their intrinsic rate of increase. These are seed reproduction and vegetative reproduction. The balance between these two components is one aspect of the life-history strategy that aims to overcome the environmental constraints on the intrinsic rate of increase (Bradshaw and Doody 1978). Vegetative propagation did not appear to be a significant component of the life-history strategy for this species. As discussed above, the genet was generally composed of a closely packed cluster of very few rosettes (ramets) or a solitary rosette. This appeared to be characteristic of a phalanx rather than guerilla strategy (Clegg 1978 in Hutchings and Bradbury 1986). Such a growth strategy is resistant to invasion by other plants. Although disturbance (primarily fire) was a relatively frequent event (1-5 year interval) in these habitats they remained highly diverse and competition for resources was likely to be high. Consequently, the

Table 7. Overall mean number of ramets and stems per genet, and mean stem height per genet in 1996.

	N	Mean ± SE	Range
Number of Ramets	1005	3 ± 0.07	1 - 22
Number of Stems	1006	1 ± 0.03	1 - 18
Mean Stem Height	1006	72.86 ± 0.46	26.20 - 119.60

phalanx strategy may be successful enough to occupy sufficient space in order to acquire resources to sexually reproduce each year and reserve some resources in the rootstock to survive unfavorable conditions. Furthermore, because the sites are nutrient limited, wetland habitats they probably remain relatively uniform over the long-term under natural disturbance regimes. Therefore, components of a life-history strategy best suited for semi-permanent habitats may be beneficial. The lifespan of individual genets is unknown. Seed dispersal would appear to be limited, but is unknown, and the extent of seed dormancy is also unknown. Nonetheless, it seems reasonable that this species may rely primarily on seed production for establishment in new populations. In fact, it is questionable whether ramets serve as true vegetative reproduction units by becoming independent from the parent plant. Ron Determann (personal communication) believes that light may be required for the seeds to germinate. Consequently, it seems likely that a moderate level of seed dormancy would be required to ensure that seeds are viable when disturbance eventually opens the vegetation cover and exposes the soil to direct sunlight. Under high light conditions in the greenhouse germination was rapid (see more on **Reproduction** below). This would be a beneficial strategy to rapidly take advantage of newly opened space and ensure population persistence. All in all, it seems reasonable that *B. atropurpurea*'s life-history strategy lies somewhere between the extremes of MacArthur and Wilson's r- and K-selected patterns (1967), and Grime's R-, C-, and S-selected patterns (1977). However, the relative role of sexual and vegetative reproduction in the population dynamics of this species needs further examination. Furthermore, monitoring the population dynamics of this species in both space and time may advance an understanding of the life-history strategy and persistence of this species.

In 1996, the number of stems per genet was relatively consistent among populations. In general, over half of the ramets per genet were stemmed; therefore, they were capable of sexual reproduction. There was 1 stem per genet on average (Table 7) with population means ranging from 1 stem per genet (population n8) to 5 stems per genet (population n7) (Figure 9). Populations n5, n7, n9, and n14 had a relatively greater number of stems per genet while population n8 had relatively fewer stems per genet than all other populations. Population n7 had only one observation that appeared to be a robust individual. No substantive meaning could be proposed for the relatively high or low means based on the characteristics of the populations. Since this species may vegetatively reproduce, the exact identity of unique genetic individuals may be difficult to discern. Furthermore, since seed dispersal is likely to be minimal, rosettes growing in close proximity may or may not be separate individuals. Therefore, monitoring the number of stems per plot or population may be more easily accomplished and more informative than monitoring genets.

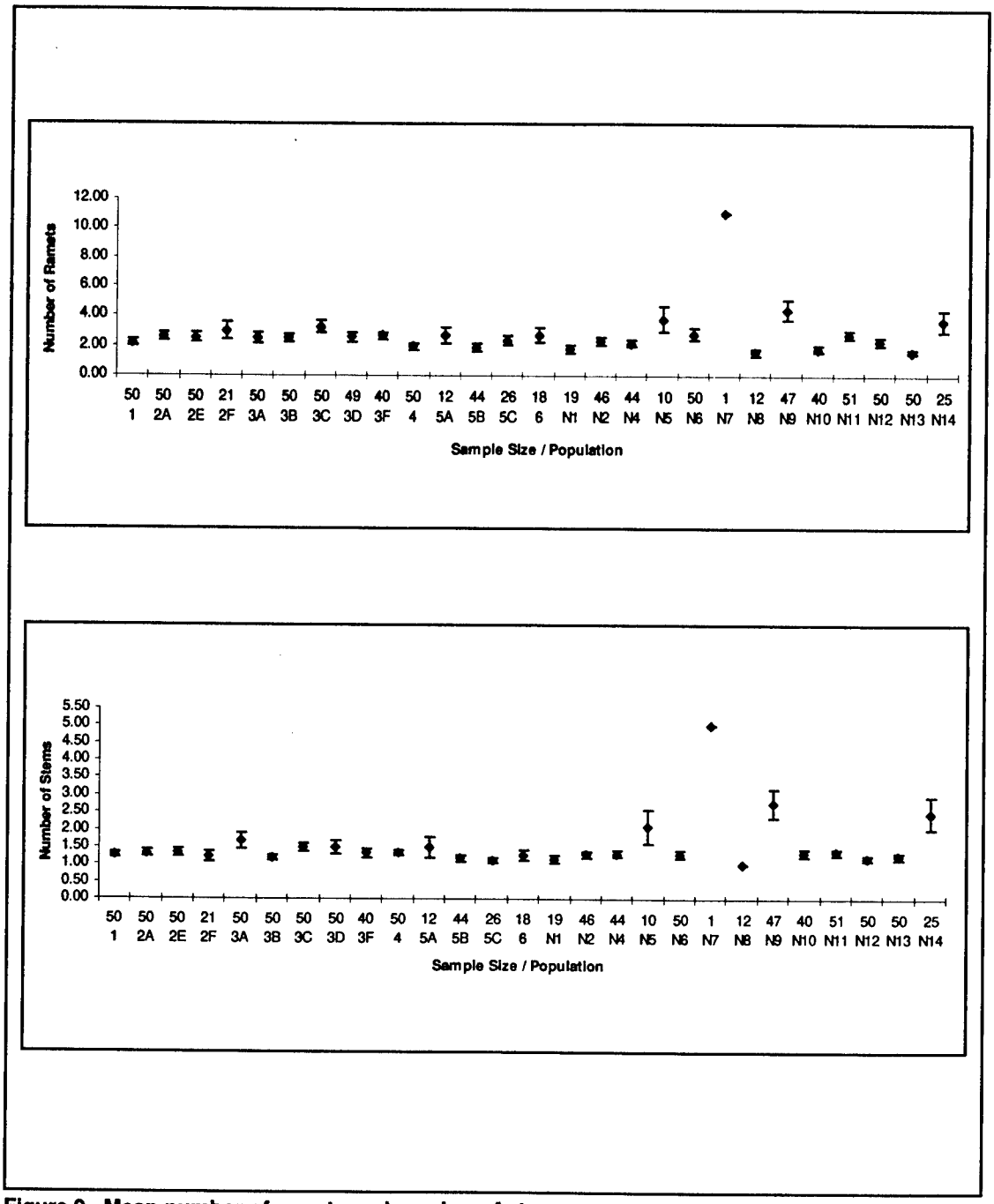


Figure 9. Mean number of ramets and number of stems per genet per population in 1996.

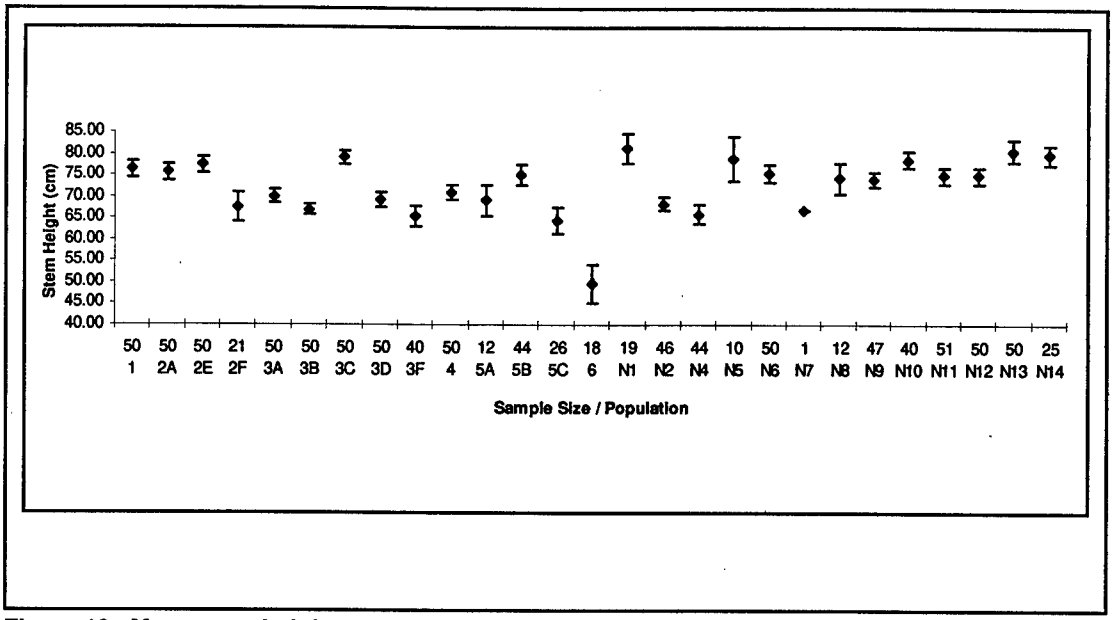


Figure 10. Mean stem height per genet per population in 1996.

In 1996, mean stem height per genet was highly variable among populations. Overall mean stem height per genet was 72.86 cm (Table 7) with population means ranging from 49.62 cm (population 6) to 81.36 cm (population n1) (Figure 10). This may reasonably be explained by the relative light level associated with each population. The populations characterized by low or moderate light levels were the populations that also had mostly low mean stem heights, although not exclusively. Population 6 had a relatively low mean stem height compared to the other populations and was the only population characterized as having a low relative light level. This population was located at the intersection of an old trail, fire plow line, and a small drainage within a pine flatwood and received very little direct sunlight. The plants in this population did indeed appear less vigorous than plants found elsewhere on Fort Stewart. However, Widen (1991a, 1993) found that shorter *Senecio integrifolius* plants were associated with sunny sites. Consequently, the variation in stem height may have been confounded by other unmeasured variables or does not have the same response to light with *B. atropurpurea*. In fact, if the basal leaves are the main photosynthetic tissues (unknown), then stem height may not be primarily a growth response to light levels, but more relevantly a component of floral display (see more discussion in **Seed Production** below). Nonetheless, mean stem height may have been the first variable that appeared to show a significant environmental response in plant vigor and to reveal population differences in habitat quality, particularly since weather conditions were similar across years (see more discussion in **Discriminant Analysis** below).

Four of the measured genet characters were correlated based on Spearman rank correlation coefficients. First, the number of stems was correlated to the number of

ramets (r=0.5739, p=0.0001, n=1005) and to the number of inflorescences (r=0.5754, p=0.0001, n=1005). Next, the number of ramets had a weak but significant correlation to the number of inflorescences (r=0.2774, p=0.0001, n=1004). Last, mean stem height had a weak but significant correlation with the number of inflorescences (r=0.3505, p=0.0001, n=1004). These correlations suggest that larger, more vigorous genets (greater number of ramets and stems, and greater stem height) produce more inflorescences and potentially contribute more to the population in terms of sexual reproduction. Larger genets may suggest healthier plants.

Reproduction

In 1995 and 1996, an assessment of floral production was conducted as a broad measure of sexual reproduction. In 1995, seed samples were collected from mature inflorescences of the sampled plants for an assessment of seed production and seed viability. On the whole, floral production was variable among populations, seed production was low, and seed viability was high. An assessment of flower pollination, seed dispersal, seed dormancy, and natural seedling emergence and establishment was not conducted. Study of these aspects of sexual reproduction may be of value in advancing the knowledge of the breeding system and life-history strategy of *B. atropurpurea*.

Floral Production

The number of inflorescences per quadrat (floral density) was variable among populations. In 1995, the estimated floral density per quadrat was 7.3 inflorescences/m^2 (Table 8) with population means ranging from 5.4 inflorescences/m^2 (population 5) to 9.7 inflorescences/m^2 (population 4) (Appendix D). In 1996, the estimated floral density per quadrat was 0.3 inflorescences/m^2 (Table 8) with population means ranging from 0.0 inflorescences/m^2 (populations 2a, 2f, n1, n2, n5, n6, n7, n8, and n11) to 0.9 inflorescences/m^2 (population n13) (Figure 11). The high values for 1995 represented a small scale or patch scale measure of inflorescence density since the quadrat was centered around the sampled genet and sampling was limited to obvious patches of plants in potentially higher quality habitat. In 1996, there was a high degree of variation in the number of inflorescences per quadrat as

shown by the wide standard errors. This was most likely the result of quadrats containing very few or very many inflorescences. The range of values was also quite large. The results for a one-way nonparametric ANOVA on the number of inflorescences per quadrat in 1996 revealed a significant difference between at least two populations (F=1.65, p=0.0231) (Table 5). However, none of the Scheffé multiple comparisons were significant. As discussed above for genet density, the large number of quadrats representing "misses" may also indicate that more sampling

Table 8. Overall mean number of inflorescences per quadrat and per genet in 1995 and 1996, and overall mean number of inflorescences per ramet in 1995.

Year	Number of Inflorescences	N	Mean ±SE	Range
1995	per Quadrat	290	7.3 ± 0.41	1 - 61
1996	per Quadrat	1006	0.3 ± 0.05	0 - 21
1995	per Genet	290	4 ± 0.19	1 - 20
1996	per Genet	1005	3 ± 0.08	1 - 27
1995	per Ramet	290	3 ± 0.10	1 - 11

quadrats were needed to more accurately estimate inflorescence density for this species. The same suggestions for improving the genet density estimates would apply to improving the floral density estimates.

Pollinators are less likely to be attracted to a population as the flowering plant density decreases (e.g., Levin and Kerster 1974; Beattie 1976; Handel 1983; Murawski and Hamrick 1991; Widen 1993; Agren 1996), inflorescence density decreases (Widen 1993), or the population size decreases (e.g., Sih and Baltus 1987; Sowig 1989; Kwak et al. 1991; Widen 1993; Fritz and Nilsson 1994; Agren 1996). Any reduction in pollinator visitation may reduce seed output (e.g., Jennerston 1988; Kwak et al. 1991; Ellstrand and Elam 1993; Fritz and Nilsson 1994; and Agren 1996). Reduced pollinator visitation is particularly important for outcrossing animal-pollinated plants that depend on pollinator visitation for seed production. The reduction in reproductive output due to such population characteristics has been termed the Allee effect in relation to animals (Lande 1988) and may have significant consequences for population persistence. Furthermore, flowering plant density and population size may influence the degree of mating between close relatives, which may result in inbreeding depression (e.g., Ellstrand, Torres, and Levin 1978; Lande 1988; Watkins and Levin 1990; Ellstrand and Elam 1993; Widen 1993; Frankel, Brown, and Burdon 1995). If pollinator flight distances are density-dependent, pollinator flight distances decrease and the level of outcrossing decreases

as flowering plant density increases (Levin and Kerster 1974; Ellstrand, Torres, and Levin 1978; Widen 1993 and references therein). One consequence of inbreeding depression is a reduction in seed production and seed viability that may increase the probability of population extinction (Lande 1988; Menges 1991; Ellstrand and Elam 1993; Frankel, Brown, and Burdon 1995). The reduction in viability as a result of inbreeding is most severe in the early stages of the life cycle (Levin 1991). Therefore, reduced seed production and seed viability may have significant consequences for the demographics of *B. atropurpurea* (see more discussion on population characteristics and reproduction in the following sections). Resource limitation may also be an important cause of reduced seed production and seed viability.

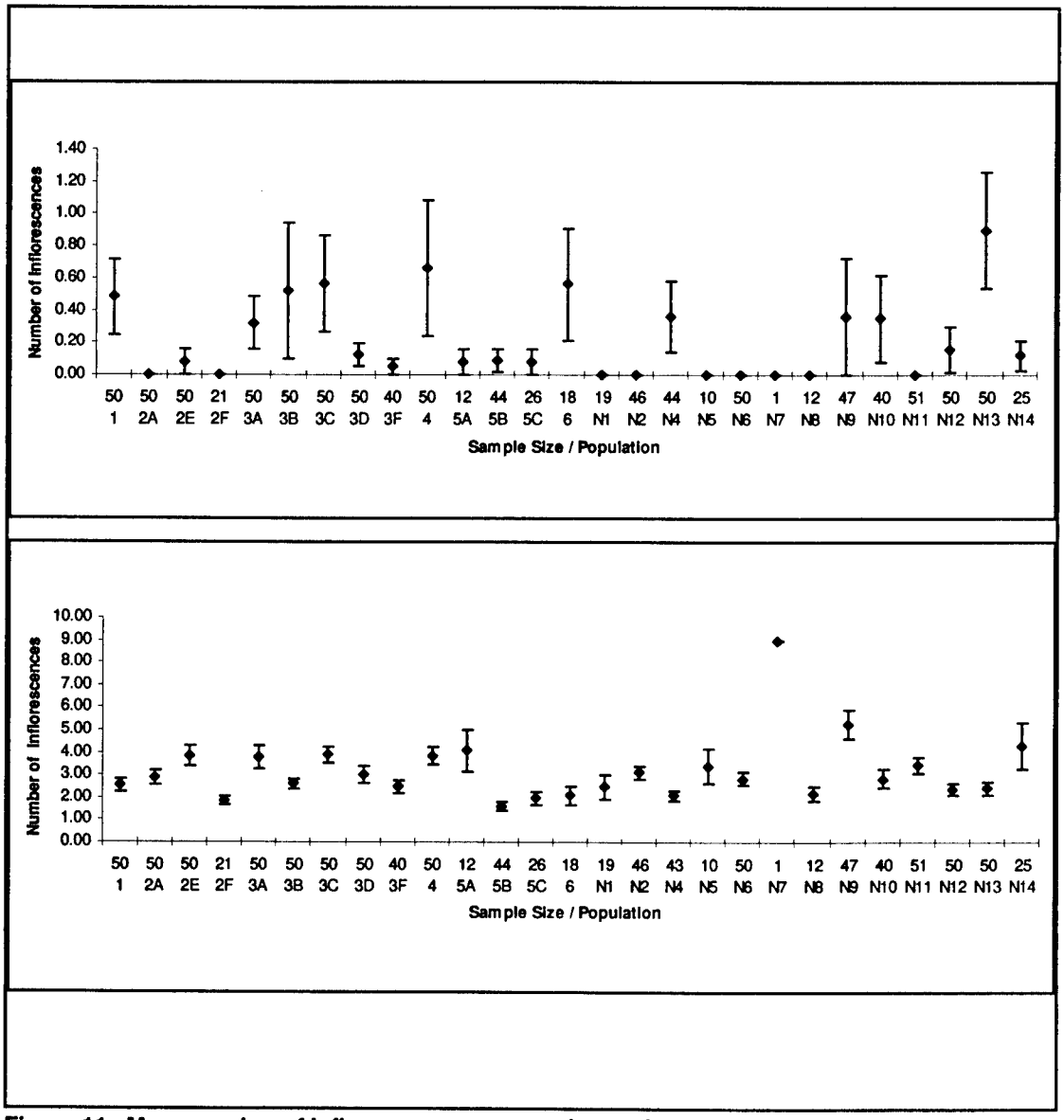


Figure 11. Mean number of inflorescences per quadrat and per genet per population in 1996.

The number of inflorescences per genet varied among populations within years (Table 8). In general, the number of inflorescences per genet exceeded the number of stems per genet. Therefore, stemmed ramets frequently had multiple branches each terminating with an inflorescence. In 1995, there were 3 inflorescences per ramet on average (Table 8) with population means ranging from 2 inflorescences per ramet (population 5) to 3 inflorescences per ramet (population 2) (Appendix D). In 1995, there were 4 inflorescences per genet on average (Table 8) with population means ranging from 3 inflorescences per genet (population 5) to 6 inflorescences per genet (population 1) (Appendix D). In 1996, there were 3 inflorescences per genet on average (Table 8) with population means ranging from 2 inflorescences per genet (population 5b) to 9 inflorescences per genet (population n7) (Figure 11). Populations 5a, n7, n9, and n14 had a relatively greater number of inflorescences per genet while populations 2f, 5b, and 5c had relatively fewer inflorescences per genet than all other populations. Population n7 had only one observation that appeared to be a robust individual. No substantive meaning could be proposed for the high or low means based on the characteristics of the populations. Nonetheless, based on the correlations discussed above, it appeared that the more vigorous genets produced more inflorescences. The exact characters that best define size for *B. atropurpurea* need further examination. Moreover, the production of a large number of inflorescences does not necessarily equate to the production of more mature seeds (see more discussion in **Seed Production** below). Monitoring the number of stems, stem height, and the number of inflorescences per stem may be enough to assess population stability and likelihood of persistence over time. However, monitoring seedling establishment, which may be more difficult, may also be needed to fully determine population stability and likelihood for population persistence.

The percent of flowering ramets was variable among populations within years. In 1995, 60% of the ramets were flowering. In 1996, 56% of the ramets were flowering while the remainder stayed in the vegetative rosette stage (Table 9). The percentage of flowering ramets ranged from 41% (population 2f) to 77% (population n13). The ratio of flowering to nonflowering ramets ranged from 0.7:1.0 (population 2f) to 3.3:1.0 (population n13) and averaged 1.3:1.0 overall. In 1995, 61% of the genets were flowering. Consequently, to the casual observer, a significant portion of the population was inconspicuous. Populations 2f, 3b, 3c, 5c, 6, n6, and n7 had a greater percentage of ramets in the vegetative stage. No substantive meaning could be proposed for the greater proportion of ramets existing in the vegetative stage, except this strategy was best suited for the environmental conditions of these populations during 1996. Nonetheless, it has been observed in other perennial herbs that the proportion of individuals within a population and ramets within an individual that are flowering and producing seeds is highly variable in any year (Inghe and Tamm 1988). Populations 2a, 3f, and n11 had an equal percentage of flowering and

vegetative ramets. Due to the difficulties associated with determining the exact composition of a genet, monitoring the proportion of the population flowering and nonflowering may be more difficult.The overall mean capitulum width per inflorescence was 2.11 cm (Table 10) with population means ranging from 2.00 cm (population 5*) to 2.15 cm (population 2) (Appendix D). There were 15 ray flowers per inflorescence on average (Table 10) with population means ranging from 14 ray flowers per inflorescence (population 5) to 16 ray flowers per inflorescence (population 1) (Appendix D). These two characters were relatively consistent among populations in 1995.

Seed Production

Seed characteristics were measured on 33 seed samples collected in the fall of 1995. The high degree of variation found in several of the following characters as shown in the standard errors was most likely due to the small sample sizes. Of the 126 inflorescences bagged to prevent seed loss, only 54 (43%) were recovered. The collection of the inflorescences was hindered because the bags blended into the vegetation and the stems often bent over, obscuring the bagged inflorescence. The weight of the bag, especially when wet, may have contributed to some stems breaking as some inflorescences were found on the ground separated from the stem.

The majority of the bagged inflorescences that were recovered remained in good condition. Several seed heads from populations 1, 2, 4, and 5 contained bore holes and/or microlepidopteran larvae. The larvae were tentatively identified as *Metzneria* sp. (Terry Harrison, University of Illinois, personal communication), an introduced moth that is known to feed on inflorescences of burdock (*Arctium* sp., Asteraceae) and reside in the Southeast. Microlepidopteran predation has also been

Table 9. Percent of flowering ramets per population and overall in 1996.

Population	1	2a	2	2f	3a	3b	3c	3d	3f	4	5a	5b	5c	6
Percent of Flowering Ramets	58	50	54	41	66	48	46	57	50	70	56	63	48	47
Population	n1	n2	n4	n5	n6	n7	n8	n9	n10	n11	n12	n13	n14	Overall
Percent of Flowering Ramets	65	56	61	55	47	45	63	63	74	50	52	77	68	56

* In 1995, the known populations were 1,2,3,4, and 5. Other populations were found in 1995. The 1996 data contains all the populations.

documented with other rare plant species (Menges, Waller, and Gawler 1986; Windus 1990). Post dispersal seed predation was not examined. All forms of seed predation may have an influence on population demographics (Cavers 1983; Menges, Waller, and Gawler 1986; Crawley 1992) and further examination of seed predation may be required to fully understand the population dynamics of this species. Inflorescence predation was observed in all populations. Furthermore, fungal infestation was observed on inflorescences in populations 2 and 3, and rotten seeds were found in samples from all populations. Six inflorescences were wet when collected, which may have contributed to the deterioration of some samples. When the samples arrived in Illinois, three of the wet inflorescences had seeds germinate directly in the heads.

Based on the Wilcoxon signed rank test (N=28, α=.05, critical value (cv)=117) there was a significant difference between the bagged and unbagged control inflorescences for total ovule number (6.0<117, T<cv), mature seed number (95<117), seed set (75<117), total seed mass (86<117), and individual seed mass (92<117), but not for proportion seedling emergence (158>117). However, all of the means were greater for the bagged samples except for seed set (30% compared to 31%). Consequently, the bags did not appear to negatively affect seed production and quality. One possible cause of reduced seed numbers and mass in the unbagged samples was the observed loss of seeds from the heads prior to collection. Use of the nylon bags may have been an acceptable technique to prevent seed loss before collection; however, their use may be limited to more rigid stemmed plants and may require additional markings to facilitate relocation.

Table 10. Mean overall capitulum width, number of ray flowers, ovule number, mature seed number, seed set, seed mass, and seedling emergence per inflorescence in 1995.

	N	Mean ± SE	Range
Capitulum Width	254	2.11 ± 0.02	1.10 - 2.80
Number of Ray Flowers	254	15 ± 0.18	2 - 23
Ovule Number	32	127 ± 5.47	49 - 198
Mature Seed Number	33	36 ± 4.65	0 - 78
Seed Set	32	0.30 ± 0.04	0.00 - 0.67
Mature Seed Mass	33	41.20 ± 5.80	0.00 - 108.60
Mean Mature Seed Mass	32	1.20 ± 0.10	0.40 - 1.90
Proportion Seedling Emergence	32	0.75 ± 0.05	0.00 - 1.00

Seed production was variable among populations. There were 127 ovules per inflorescence on average (Table 10) with population means ranging from 105 ovules per inflorescence (population 4) to 155 ovules per inflorescence (population 1) (Figure 12). There were 36 mature (filled) seeds per inflorescence on average (Table 10) with population means ranging from 18 seeds per inflorescence (population 5) to 54 seeds per inflorescence (population 3) (Figure 12B). The overall mean seed set (the proportion of the total number of ovules that were mature seeds) was 0.30 (Table 10) with population means ranging from 0.12 (population 5) to 0.48 (population 3) (Figure 12C). The lower seed set implied that a considerable number of seeds were possibly aborted or never filled. No relationship between total ovule number and mature seed number was found based on Spearman rank correlation ($r=0.0298$, $p=0.8713$, $n=32$), although Figure 12A and 12B suggested that a greater number of total ovules per inflorescence resulted in a lower number of mature seeds. The overall low number of mature seeds may be due to resource limitation or lack of pollination. Population 3 had a relatively high seed set compared to the other populations. Widen (1991a, 1993) found that in sunny habitats the *Senecio integrifolius* plants were shorter, had fewer inflorescences, and flowered earlier than tall plants growing in shadier habitats. This resulted in lower seed set for the taller plants probably as a result of decreasing flower density and reduced pollinator visitation (an indirect influence of environmental conditions on flowering phenology) (Widen 1991b, 1993). Population 3 was the more open of the habitats and had the lowest mean plant height in 1995; however, it had the second lowest number of inflorescences per genet. Ramet height was also negatively related to seed set based on Spearman rank correlation ($r=-0.4229$, $p=0.0159$, $n=32$) and positively related to the number of inflorescences per ramet ($r=0.4176$, $p=0.0156$, $n=33$), although both correlations were weak. However, there was a weak, insignificant, negative relationship between the number of inflorescences per ramet and seed set based on Spearman rank correlation ($r=-0.2423$, $p=1816$, $n=32$). Nonetheless, this may be a reasonable explanation for the high seed set. The large standard errors indicated that a greater sample size was needed to more accurately estimate mean seed production for this species.

Seed set did not exceed 50% in these five populations and was relatively low compared to other rare composites (e.g., Les, Reinartz, and Esselman 1991; Widen 1993). The number of mature seeds per inflorescence and per plant was relatively moderate and consistent with a plant occupying mid-successional habitats. A positive relationship was found between population size and seed set based on Spearman rank correlation ($r=0.5396$, $p=0.0001$, $n=32$) and has been observed in other plants (Widen 1993; Jennersten 1988; Byers and Meagher 1992). However, there was no relationship between seed set and genet density based on Spearman rank correlation ($r=-0.1076$, $p=0.5579$, $n=32$). Moreover, there was no relationship

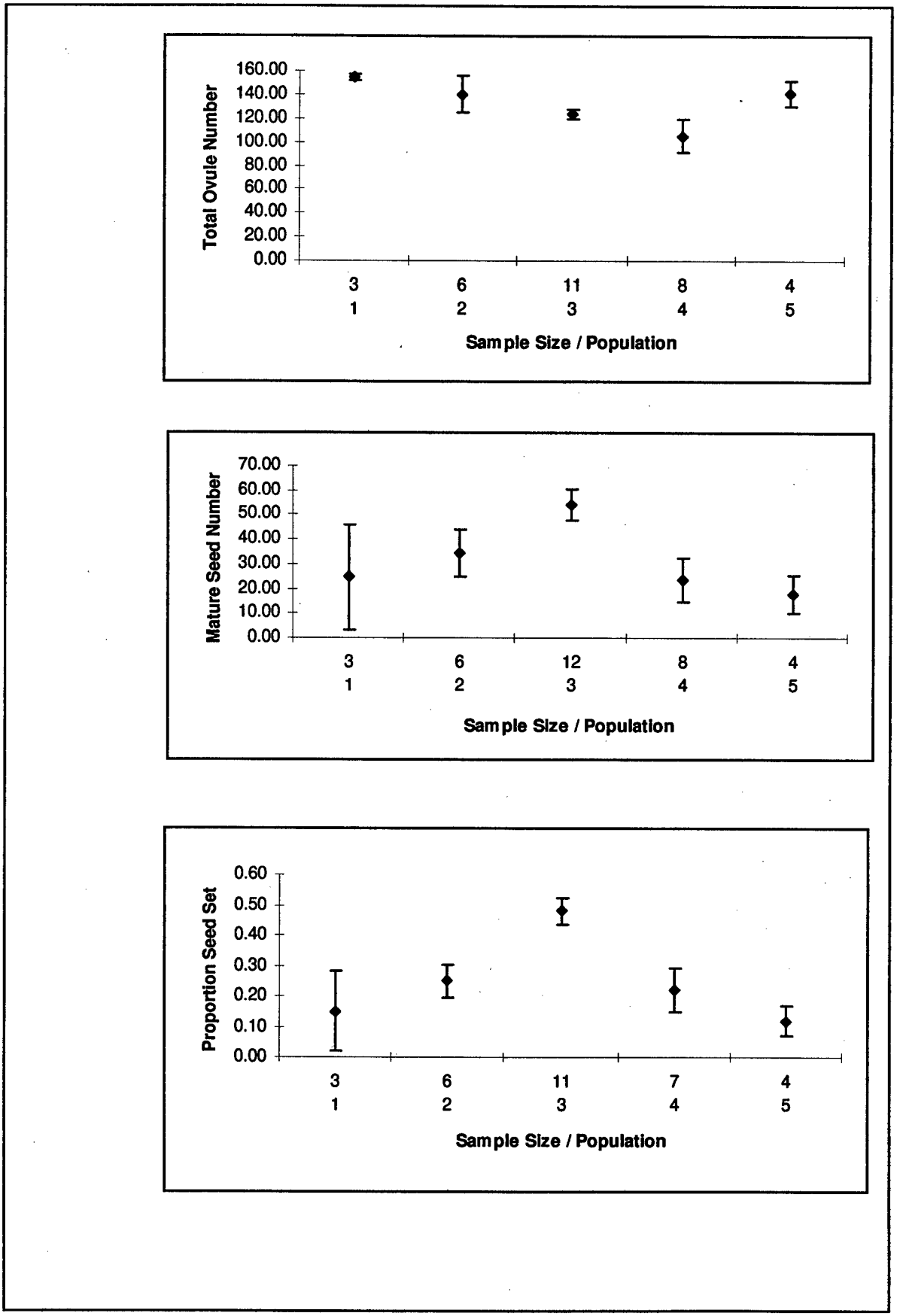


Figure 12. Mean total ovule number, mature seed number, and proportion seed set per inflorescence per population in 1995.

based on Spearman rank correlation between seed set and the number of ramets per genet (r=0.1368, p=0.4552, n=32), the number of stems per genet (r=0.1175, p=0.5217, n=32), or the number of inflorescences per genet (r=0.0226, p=0.9022, n=32). That is, seed set appeared not to be related to plant size. This contradicts the general observation that the reproductive allocation in perennials, which is influenced by environmental conditions and competition, increases with plant size (Bazzaz and Ackerly 1992 and references therein; Crawley 1992). A larger sample size and better understanding of the characters that best determine size in *B. atropurpurea* are probably needed to clarify these relationships between plant size and seed production. In contrast, Widen (1993) found a negative correlation between seed set and floral display (inflorescence height, corymb size). Negative Spearman rank correlations were also found between seed set and ramet height (significant), number of inflorescences (not significant), capitulum width (r=-0.3065, p=0.0880, n=32), and number of ray flowers (r=-0.5498, p=0.0011, n=32), although weak. It appeared that seed production and seed set in *B. atropurpurea* may be more related to population size and possibly flowering phenology than to plant size.

Seed mass was also variable among populations. The overall mean mature seed mass per inflorescence was 41.2 mg (Table 10) with population means ranging from 22.2 mg (population 5) to 54.2 mg (population 3) (Figure 13). The very large standard errors indicated that seed mass was extremely variable and that a much greater sample size was needed to accurately estimate total seed mass. However, total inflorescence seed mass was related to the mature seed number per inflorescence, which was also highly variable among inflorescences, based on Spearman rank correlation (r=0.9439, p=0.0001, n=32). The reasons for the high variation in seed production were discussed above. The overall mean individual mature seed mass per inflorescence was 1.2 mg (Table 10) with population means ranging from 1.0 mg (population 3) to 1.3 mg (populations 2 and 4) (Figure 13). The mean seed mass was relatively small compared to other composites (e.g., Gross 1984; Banovetz and Scheiner 1994), but may be considered a medium sized seed (Harper 1977) characteristic of a plant inhabiting mid-successional habitats. Population 3 had a relatively low mean individual mature seed mass compared to the other populations. This population also had a greater number of mature seeds per inflorescence on average. It is reasonable that the lower individual seed mass represents a tradeoff between seed number and seed mass (Harper, Lovell, and Moore 1970; Bazzaz and Ackerly 1992) and again is compatible with a species inhabiting mid-successional habitats. Mean individual seed mass was less variable; however, the standard errors still implied that a greater sample size was needed to accurately estimate mean seed mass.

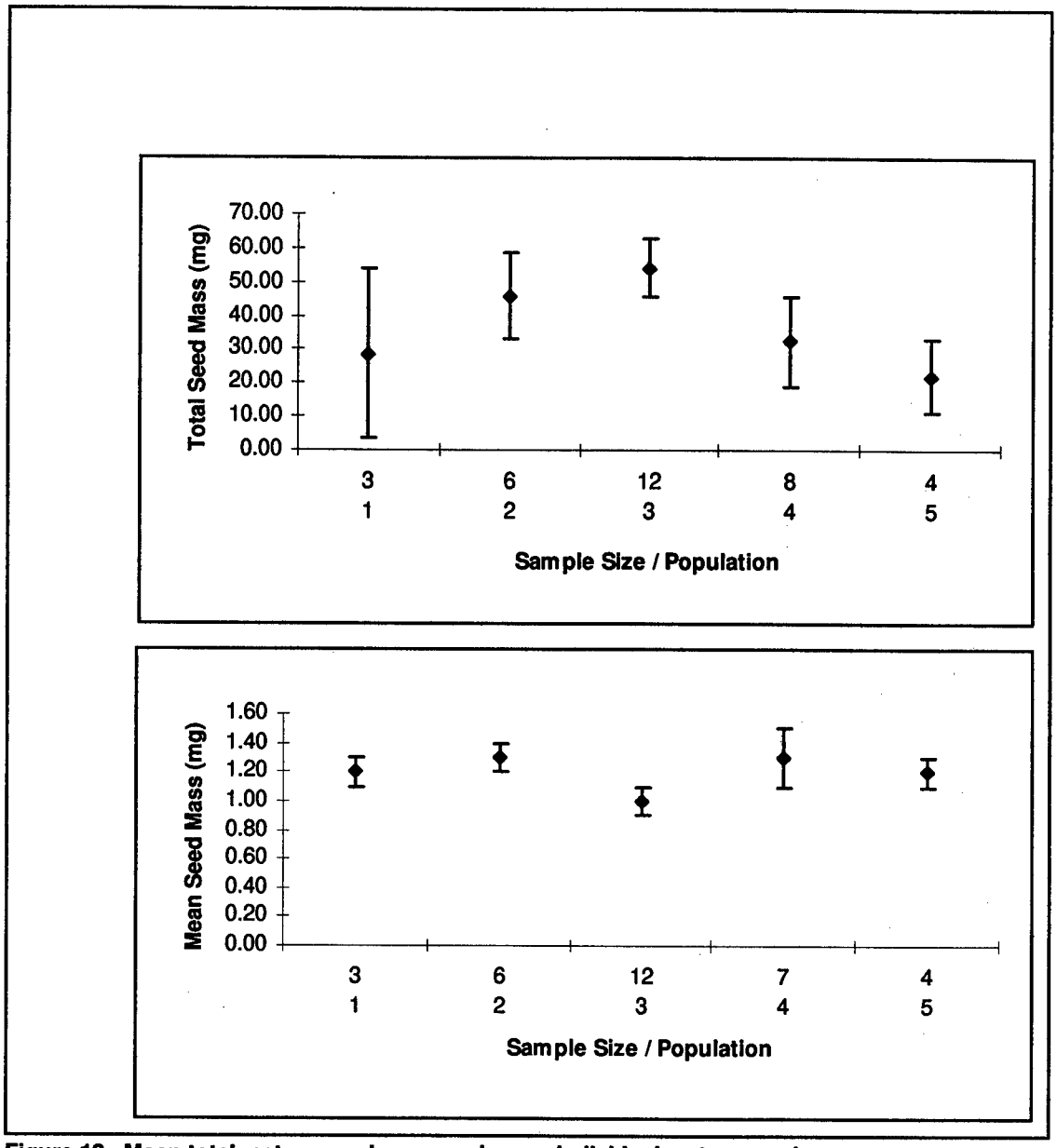


Figure 13. Mean total mature seed mass and mean individual mature seed mass per inflorescence in 1995.

Seed Viability

Ron Determann of the Atlanta Botanical Garden conducted the seed viability test, during the winter and early spring of 1996, on the seeds collected in the fall of 1995. After the 4-week stratification, where no seedling emergence was observed in the cooler, the seeds were sown and seedling emergence was observed in the greenhouse for 14 days. The seeds had reasonably high viability and the seedlings were generally healthy. Mold was observed on some seedlings from all populations. Nonviable seedlings (lacking chlorophyll) were observed in samples from populations 1, 3, and 4. The lack of chlorophyll may have represented signs of inbreeding

depression (Widen 1993). Seedlings with three cotyledons, which may also have been a sign of inbreeding, were observed in samples from populations 1, 2, and 4.

Seed viability was high for those populations sampled in 1995. The mean proportion seedling emergence on day 14 in the greenhouse was variable among populations. The overall mean proportion seedling emergence on day 14 was 0.75 (Table 10) with population means ranging from 0.46 (population 5) to 0.97 (population 1) (Figure 14 and Figure 15). The mean proportion seedling emergence in the greenhouse was relatively high compared to other composites (e.g., Gross 1984; Samfield, Zajicek, and Cobb 1991; Widen 1993; Banovetz and Scheiner 1994; and Hutchings and Booth 1996). A high mean individual seed mass appeared to result in a high proportion of seedling emergence, although no significant Spearman rank correlation was observed (r=0.1172, p=0.5230, n=32). However, the proportion seedling emergence was much lower in population 5. The lower proportion of seedling emergence observed in population 5 may have been due to the wet conditions in which the seeds were collected and shipped back to Illinois. It was in this population where rotten seeds and the germination of seeds in the heads upon arrival in Illinois was observed. On the other hand, a high seed set appeared to result in a lowered proportion seedling emergence, although no significant Spearman rank correlation was observed (r=-0.2377, p=1980, n=31). Although these observations were not significant, they further suggested a resource allocation tradeoff between seed number and seed size (and seedling emergence). The intermediate seed number and seed size associated with *B. atropurpurea,* and the relatively high seedling emergence are consistent with a plant inhabiting mid-successional habitats. Of course, the proportion of seedling emergence under natural conditions would be more informative in relation to the success of this aspect of this plant's life-history strategy. It would also be informative to assess seed dormancy and how seed

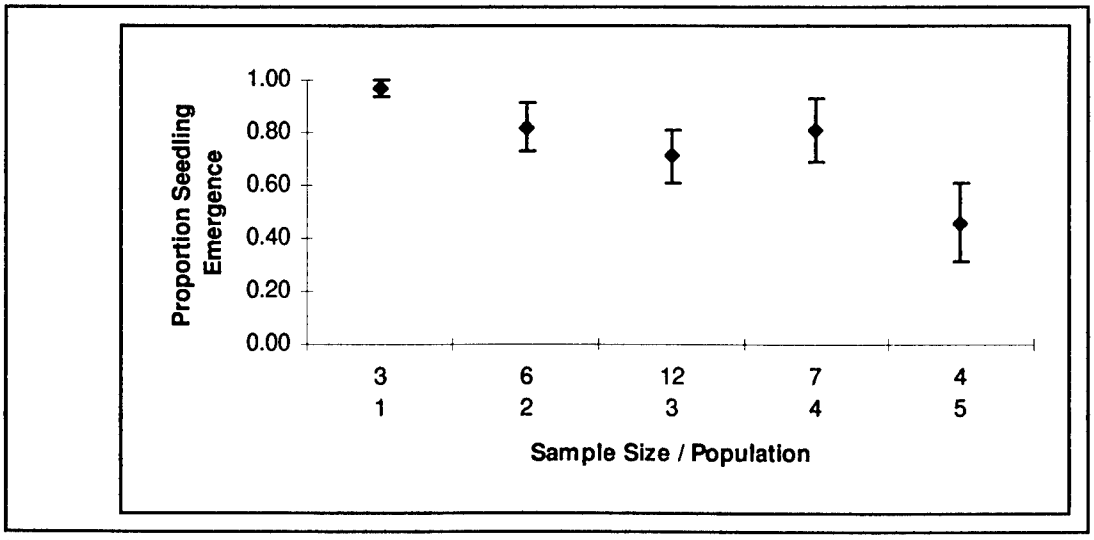


Figure 14. Mean proportion seedling emergence in the greenhouse per population in 1995.

viability changes through time for these species, particularly since it inhabits a habitat that experiences periodic disturbance. Furthermore, it would be informative to examine the timing and duration of seedling emergence throughout the year, particularly in response to disturbance events.

The daily and cumulative daily proportion seedling emergence in the greenhouse were variable among populations. No seedling emergence in the greenhouse was observed until day 2 (Figure 15). All of the populations had relatively rapid initial seedling emergence. The overall mean daily proportion seedling emergence peaked on day 4 with 17% of the seedlings emerging. Variation in the day of peak seedling emergence existed among the populations. Population 4 had the earliest peak on day 2 with 31% of the seedlings emerging, and population 5 had the latest and lowest peak on day 5 with 11% of the seedlings emerging (Figure 15A). No substantive meaning could be applied to the population differences, particularly with respect to mean individual seed mass. The exposure to the 24-hr light regime after day 6 for populations 1, 4, and 5 did not appear to have any influence on seedling emergence. The seeds from population 5 were in the worst condition when received in Illinois (as described above) and may have contributed to their relatively poor performance. In general, seedling emergence peaked in the early days and then gradually tapered off to completion. However, seedling emergence was more evenly distributed in populations 3 and 5. Although not shown, the standard errors were relatively large and once again indicated that a greater sample size was needed to more accurately characterize seedling emergence.

The rate of seedling emergence in the greenhouse was most rapid between days 2 and 5 (Figure 15) with 50% of the seedlings emerging on average by day 4 (Table 11). The overall pattern of seedling emergence was comparable to those of other plant species (e.g., Gross 1984; Samfield, Zajicek, and Cobb 1991; Widen 1993; Hutchings and Booth 1996). Populations 4 and 1 had the most rapid rates of seedling emergence with 50% of the seedlings emerging on average by day 3 (Table 11). Population 3 had the slowest rate of seedling emergence with 50% of the seedlings emerging on average by day 5 (Table 11). Seedling emergence was essentially completed on day 11, but ranged from day 8 (population 5) to day 14 (population 1) (Figure 15A and 15B). Population 3 had the largest mean number of mature seeds and the lowest mean individual seed mass but also had the slowest emergence rate. Plants in population 3 also had the shortest mean stem height as discussed above. Moreover, population 3 also had relatively small sized plants in relation to the number of ramets, number of stems, and basal leaf lengths. Although smaller plants appeared to have lower individual seed mass (and greater seed set), they also had slower emergence rates. Widen (1993) proposed that a reduced level of outcrossing led to this difference between small and large plants in *Senecio*

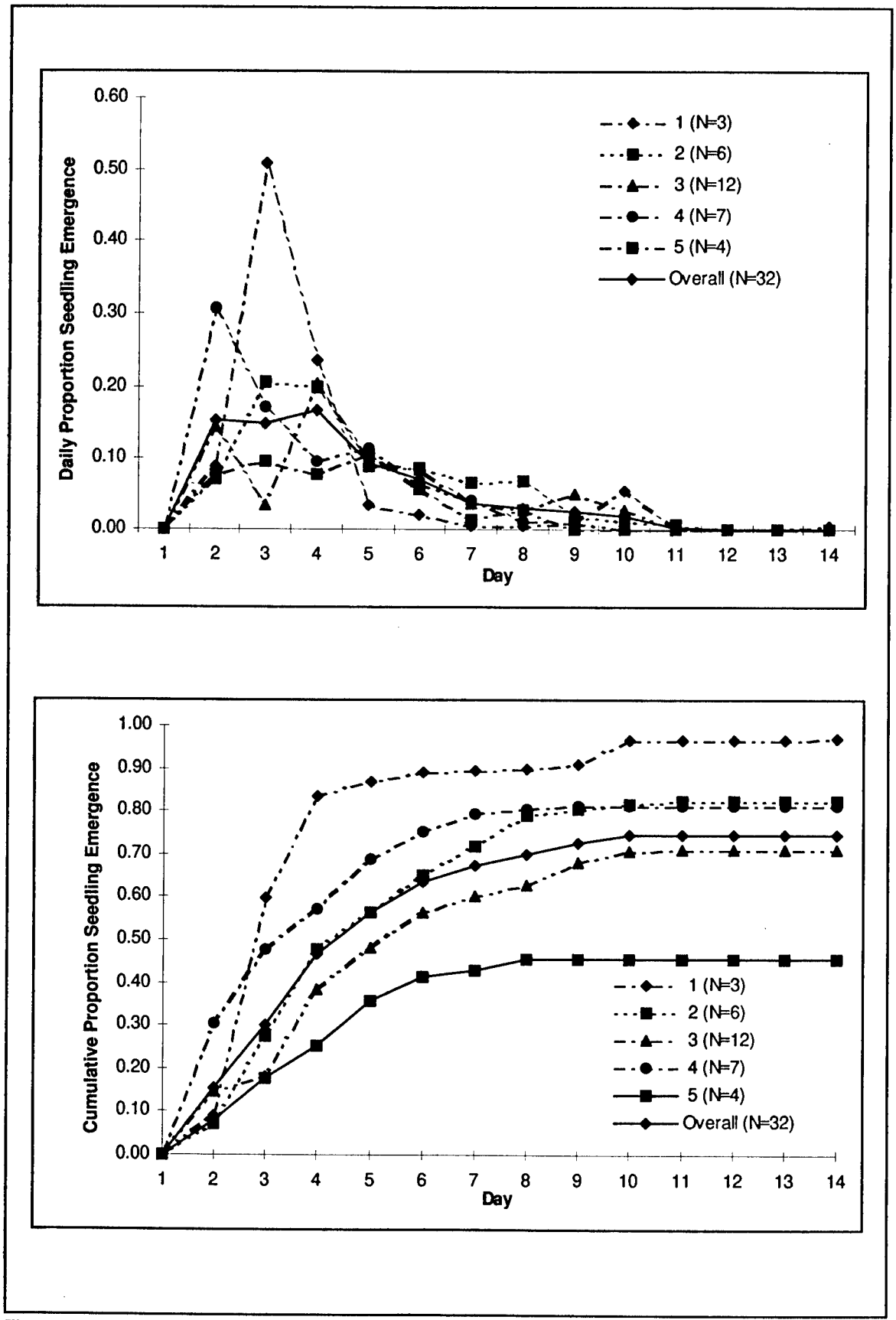


Figure 15. Mean daily proportion seedling emergence and cumulative daily proportion seedling emergence in the greenhouse per population and overall in 1995.

Table 11. Mean number of days until 50 percent seedling emergence (T_{50}) per population and overall in 1995.

Population	N	Mean ± SE	Range
1	3	3 ± 0.33	3 - 4
2	6	4 ± 0.47	3 - 6
3	12	5 ± 0.22	4 - 6
4	7	3 ± 0.36	2 - 5
5	4	4 ± 0.41	3 - 5
Overall	32	4 ± 0.17	2 - 6

integrifolius. He stated that large plants flowered later than small plants and were generally separated by greater distances; therefore, they were more likely to have a greater degree of outcrossing (Widen 1991a, 1991b, 1993). Finally, the relatively rapid seedling emergence rate and intermediate seed size were compatible with a plant inhabiting mid-successional habitats. Once again, the relatively large standard errors indicated that a larger sample size was needed to more accurately estimate seedling emergence rate. It would also be informative to examine the rate of seedling emergence under natural conditions after a disturbance event in order to advance an understanding of *B. atropurpurea's* population dynamics and life-history strategy.

Phenology

Based on field observations in 1995 and 1996 a phenological time line for major, seasonal life-history events was constructed (Figure 16). Due to logistical constraints, field observations were limited to snapshots scattered throughout the growing season. No field observations were made from December to May. As a result, the timing of some stages was conjecture.

Rosette growth was believed to occur primarily during the growing season from mid-March to late October. However, composites with basal rosettes may remain vegetative and photosynthetic throughout the winter (Walker and Peet 1983). Stem elongation, or bolting, appeared to begin in early to mid-June and continued through September, which was the peak flowering stage. Flowering was initiated in mid-August and continued into early October. Seed dispersal, which appeared to be mediated by gravity or animal movement, began late in the flowering period for early flowering individuals and probably occurred mostly during the late fall and into the following spring. Human activity may also serve as a dispersal agent. Vertical stems with intact heads containing some seeds were observed the following growing season. Seed dispersal was most likely limited to short distances and probably contributed to the aggregated distribution of individuals.

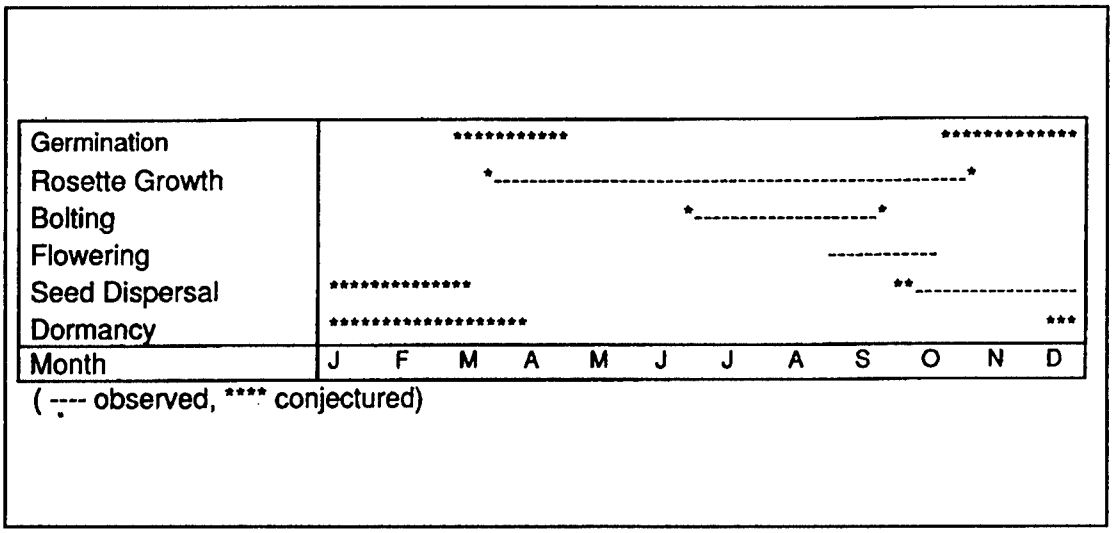


Figure 16. Mean daily proportion seedling emergence and cumulative daily proportion seedling emergence in the greenhouse per population and overall in 1995.

The use of prescribed fire to control woody vegetation and possibly promote regeneration from the seed bank should occur before stem elongation and after seed dispersal in most years. It is recognized that the historical fire regime probably included fires during the growing season, which may be required to meet other management goals. Any fire will probably be better than no fire at all. However, if a growing season fire must be conducted, it should be considered to burn only part of the management unit at any time in order to prevent a total loss of seed production. Historical fires were most likely heterogenous in both time and space. Consequently, prescribed fire management should mimic this natural variation.

Environmental Data

In 1996, a qualitative assessment of three environmental condition variables — disturbance type, relative disturbance degree, and relative light level — was completed on each sampled quadrat. Figure 17, Figure 21 and Appendix E summarize an overall assessment of the environmental condition of the *B. atropurpurea* populations. The populations were characterized as having been influenced by natural disturbance (including prescribed fire), having a low degree of disturbance, and having a high relative light level. Nonetheless, there were populations that did not fare well in regard to one or more of the environmental condition variables. The main concern was for populations with a high degree of disturbance and/or a low relative light level.

Disturbance Type

Disturbance type was categorized as natural (N) or human (H). Natural disturbance primarily referred to fire, animal disturbance, and other natural events. Human disturbance primarily referred to military ORV traffic, RCW cavity tree management, road maintenance, bivouac sites, foot traffic, extractive land uses, and other human activities. There was nearly an even number of quadrats characterized as having natural or human disturbance. This suggested that human disturbance, primarily military ORV traffic, may be a significant threat to the integrity of *B. atropurpurea* populations. Overall, 519 (52%) of the sampled quadrats were classified as natural disturbance, and 487 (48%) quadrats were classified as human disturbance (Figure 17 and Appendix E). Eighteen of the 27 populations (67%) were dominated by quadrats classified as natural disturbance. Population 2e had an equal number of quadrats classified as natural and human disturbance. Populations 3a, 4, 5c, n2, n6, n8, n10, and n14 were dominated by quadrats classified as human disturbance (Appendix E). These eight populations should be monitored closely to ensure the level of human disturbance does not become so severe that it significantly threatens population persistence. In fact, human disturbances should be monitored for all populations.

Overall means for quadrats sorted by disturbance type are shown in Figure 18. For human disturbance, the overall mean number of genets and inflorescences per quadrat were 0.27 genets/m^2 and 0.2 inflorescences/m^2. In comparison, for natural disturbance, the overall mean number of genets and inflorescences per quadrat were 0.34 genets/m^2 and 0.3 inflorescences/m^2. Based on the results of separate one-way nonparametric ANOVAs on the number of genets per quadrat ($F=1.22$, $p=0.2705$) and the number of inflorescences per quadrat ($F=0.23$, $p=0.6299$), there were no significant differences between the disturbance types (Table 12). These results suggest that as long as the disturbance was not too severe it may not make much difference to the persistence of the populations whether the disturbance was natural or human. This 1-year study characterized the visible disturbance at that time, yet the distribution and abundance of *B. atropurpurea* may be partly due to the cumulative effects of past disturbance that may no longer be visible. More study is needed to determine the exact effects various human disturbances may have on population persistence over time and should therefore be monitored annually.

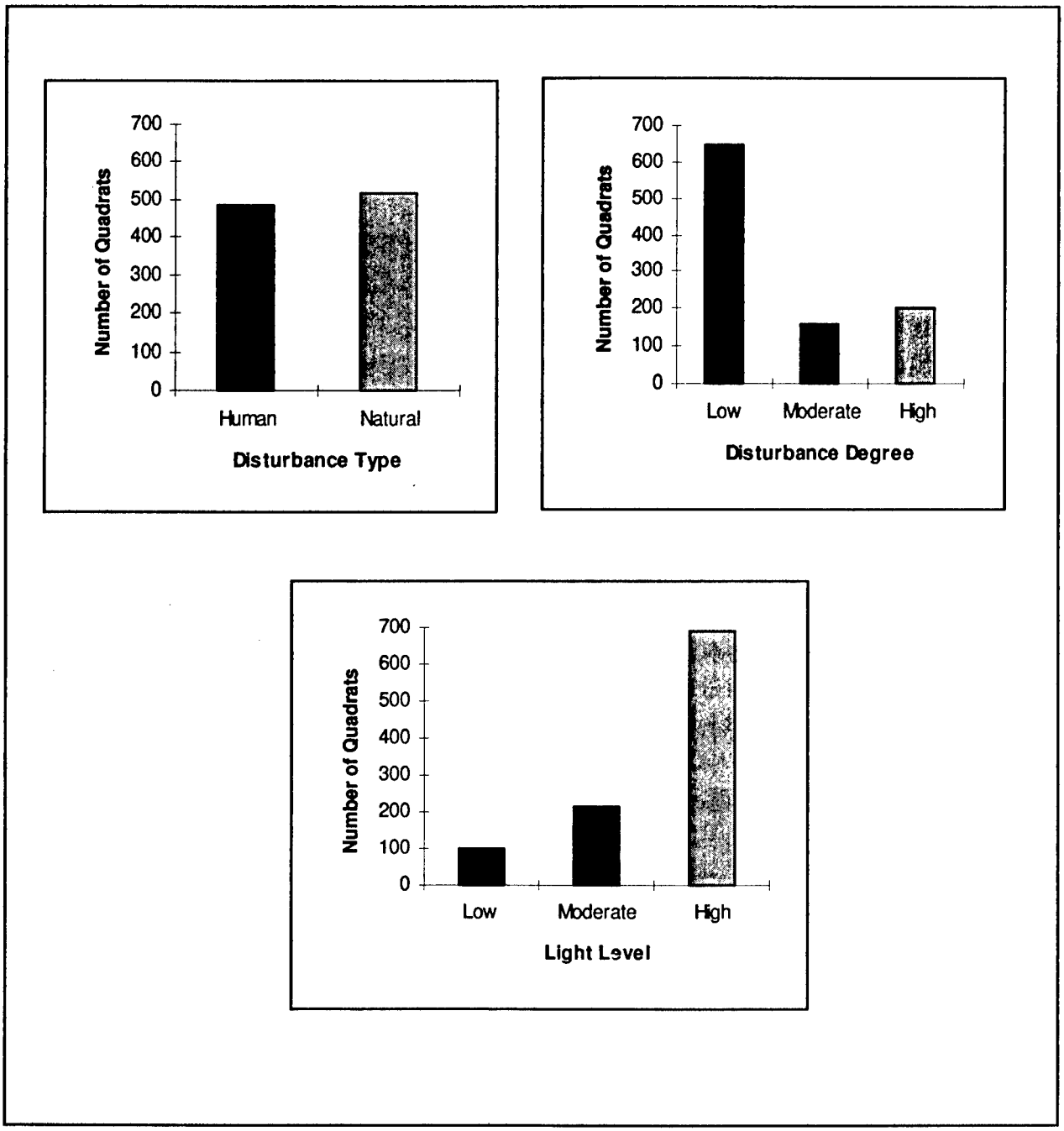


Figure 17. Overall number of sampled quadrats classified per disturbance type, disturbance degree, and light level in 1996.

Table 12. One-way nonparametric ANOVA comparisons of the number of genets per quadrat and the number of inflorescences per quadrat among the disturbance type, disturbance degree, and light level classes in 1996 (N=1006).

	Variable	F	Numerator DF	Denominator DF	P
Disturbance Type	Genets per Quadrat	1.22	1	1004	0.2710
	Inflorescences per Quadrat	0.23	1	1004	0.6299
Disturbance Degree	Genets per Quadrat	3.47	2	1003	0.0310
	Inflorescences per Quadrat	1.17	2	1003	0.3096
Light Level	Genets per Quadrat	1.81	2	1003	0.1642
	Inflorescences per Quadrat	1.23	2	1003	0.2937

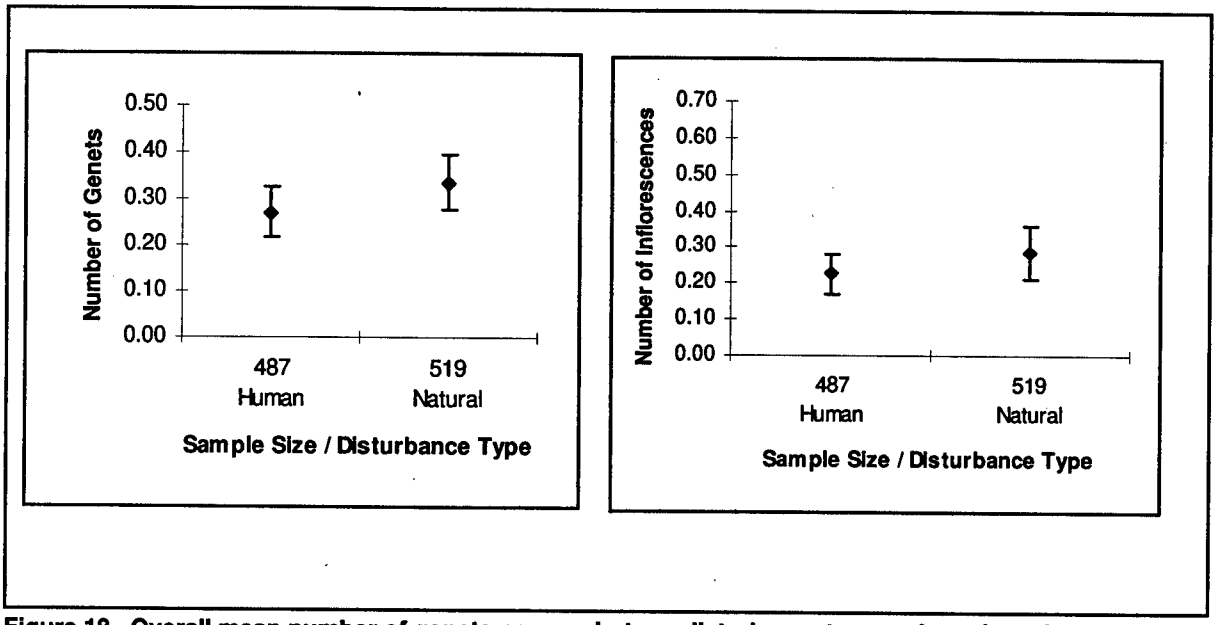


Figure 18. Overall mean number of genets per quadrat per disturbance type and number of inflorescences per quadrat per disturbance type in 1996.

Disturbance Degree

Disturbance degree was categorized as low (1), medium (2), or high (3). Low disturbance degree was characterized by little or no physical signs of alteration, moderate disturbance degree by some physical signs of alteration but not too severe, and high disturbance degree by severe physical signs of alteration to the soil or vegetation. Overall, 646 (64%) of the sampled quadrats were classified as low degree disturbance, 158 (16%) quadrats were classified as moderate degree disturbance,

and 202 (20%) quadrats were classified as high degree disturbance (Figure 17 and Appendix E). Twenty-one of the 27 populations (78%) were dominated by quadrats classified as low disturbance. Population n10 had slightly more quadrats classified as moderate disturbance. Populations 3a, 4, n2, and n14 were dominated by quadrats classified as high disturbance (Appendix E). C. Helton (in prep) reported a high level of disturbance in populations n2, n3 (which was not found again in 1996), n6, and n11. It is believed that population n3 may have been eliminated due to severe military ORV traffic. Populations characterized by a high degree of disturbance should be monitored closely to ensure that the level of disturbance does not become so severe that it threatens population persistence (see more in **Recommendations** below).

Overall means for quadrats sorted by disturbance degree are shown in Figure 19. For low disturbance degree, the overall mean number of genets and inflorescences per quadrat were 0.34 genets/m^2 and 0.2 inflorescences/m^2. In comparison, for moderate disturbance degree, the overall mean number of genets and inflorescences per quadrat were 0.36 genets/m^2 and 0.4 inflorescences/m^2. Furthermore, for high disturbance degree, the overall mean number of genets and inflorescences per quadrat were 0.15 genets/m^2 and 0.2 inflorescences/m^2, respectively. The results of a one-way nonparametric ANOVA on the number of genets per quadrat revealed a significant difference between at least two of the disturbance degree levels (F=3.47, p=0.0313) (Table 12). The Scheffé multiple comparisons showed a significant difference between the high disturbance degree and moderate disturbance degree levels (α=0.05, df=1003, MSE=23,446.33, n=1006), but no significant difference

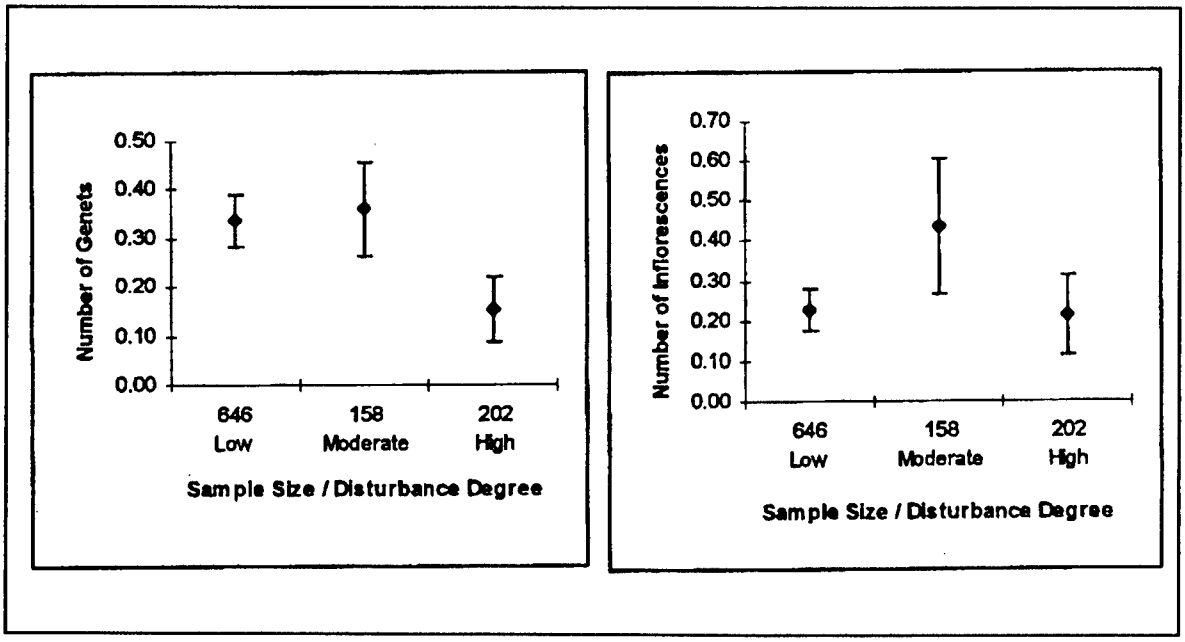


Figure 19. Overall mean number of genets per quadrat per disturbance degree and number of inflorescences per quadrat per disturbance degree in 1996.

between the high disturbance degree and low disturbance degree levels, or between the moderate disturbance degree and low disturbance degree levels. There was no significant difference among the disturbance degree levels for the number of inflorescences per quadrat (F=1.17, p=0.3096) (Table 12). However, the data suggest that a high level of disturbance may have a negative effect on the number of individuals present in a population, but not necessarily on the number of inflorescences that are produced in a population. Nonetheless, more study is needed to determine the exact effects various degrees of disturbance may have on population persistence over time and should therefore be monitored closely.

Light Level

Light level was categorized as low (shaded) (1), moderate (part sun) (2), or high (full sun) (3). Low light level was characterized by a significant degree of shading, moderate light level by some degree of shading but not too significant, and high light level by little or no degree of shading at or near the ground surface. Overall, 100 (10%) of the sampled quadrats were classified as low light level, 216 (21%) quadrats were classified as moderate light level, and 690 (69%) quadrats were classified as high light level (Figure 17 and Appendix E). Twenty-one of the 27 populations (78%) were dominated by quadrats classified as high light level. Populations 2f, 5a, n4, n7, and n14 were dominated by quadrats classified as moderate light level, and population 6 was dominated by quadrats classified as low light level (Appendix E). The relatively low level of light observed in these populations, which was a problem in portions of all *B. atropurpurea* populations, was primarily due to shrub and tree invasion. Consequently, the succession of these habitats from open bog or savanna habitat towards shrub bog or pine woodland should be monitored closely to ensure that the level of light reaching the herb layer does not become too low to threaten population persistence. Fire is believed to be the primary natural agent responsible for maintaining the open conditions of these habitats and should be used to improve the condition of *B. atropurpurea* populations that are being overtaken by shrubs and/or trees. The exact timing, frequency, duration, and intensity of fire best suited for these habitats is unknown. Therefore, the effects of any fire prescription should be monitored closely to ensure that there are no unexpected negative effects on population persistence.

Overall means for quadrats sorted by light level are shown in Figure 20. For low light level, the mean number of genets and inflorescences per quadrat were 0.27 genets/m^2 and 0.1 inflorescences/m^2. In comparison, for moderate light level, the mean number of genets and inflorescences per quadrat were 0.27 genets/m^2 and 0.2 inflorescences/m^2. Finally, for high light level, the mean number of genets and inflorescences per quadrat were 0.32 genets/m^2 and 0.3 inflorescences/m^2. Based on

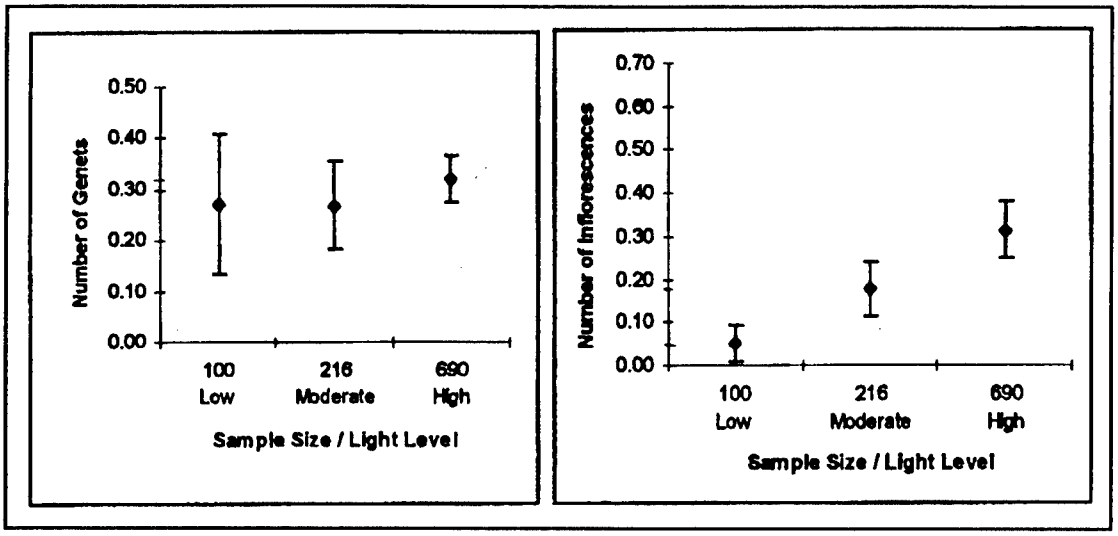


Figure 20. Overall mean number of genets per quadrat per light level and number of inflorescences per quadrat per light level in 1996.

the results of separate one-way nonparametric ANOVAs for the number of genets per quadrat (F=1.81, p=0.1642) and the number of inflorescences per quadrat (F=1.23, p=0.2937), there were no significant differences between the light levels (Table 12). However, the data suggest that high light conditions were more conducive to greater floral production. Nonetheless, more study is needed to determine the exact effect various light levels may have on population persistence over time and should therefore be monitored closely.

Disturbance Type and Disturbance Degree

The most common disturbance type plus disturbance degree combination was natural-low disturbance; 496 quadrats (49%). The least common was natural-high disturbance; 4 quadrats (0.4%). The most common human disturbance plus disturbance degree combination was human-high disturbance, 198 quadrats (20%) (Figure 21 and Appendix E). A χ^2 test for independence for disturbance type by disturbance degree was significant (χ^2=426.225, p=0.001, df=2) meaning that the variables were dependent. The data suggest that human activity was more likely to result in a greater degree of disturbance. Twenty-one of the 27 populations (78%) were dominated by quadrats classified as natural-low degree disturbance. Population n8 had more quadrats classified as human-low degree disturbance, while population n10 had more quadrats classified as human-moderate degree disturbance. Populations 3a, 4, n2, and n14 were dominated by quadrats classified as human-high degree disturbance (Appendix E). These six populations should be monitored closely to ensure that the level of disturbance does not become so severe that it threatens population persistence. No interactions were tested between

human-high degree disturbance (Appendix E). These six populations should be monitored closely to ensure that the level of disturbance does not become so severe that it threatens population persistence. No interactions were tested between disturbance type and disturbance degree for the number of genets per quadrat or the number of inflorescences per quadrat.

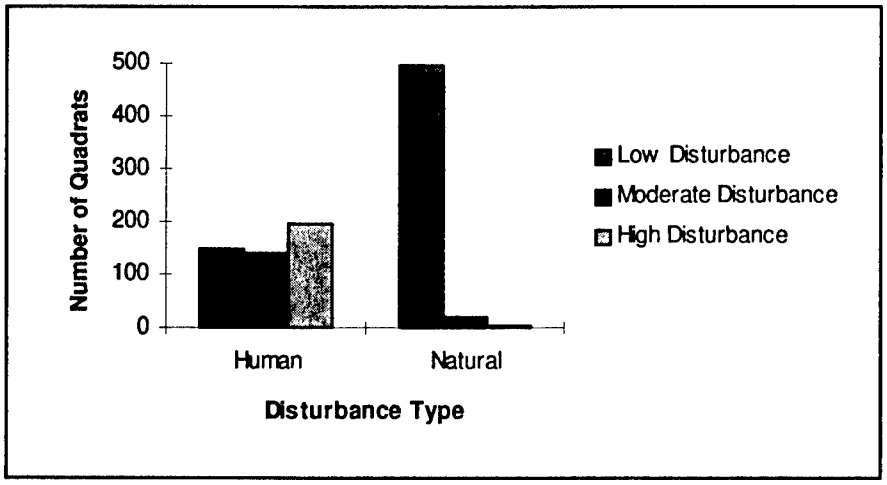
Disturbance Type and Light Level

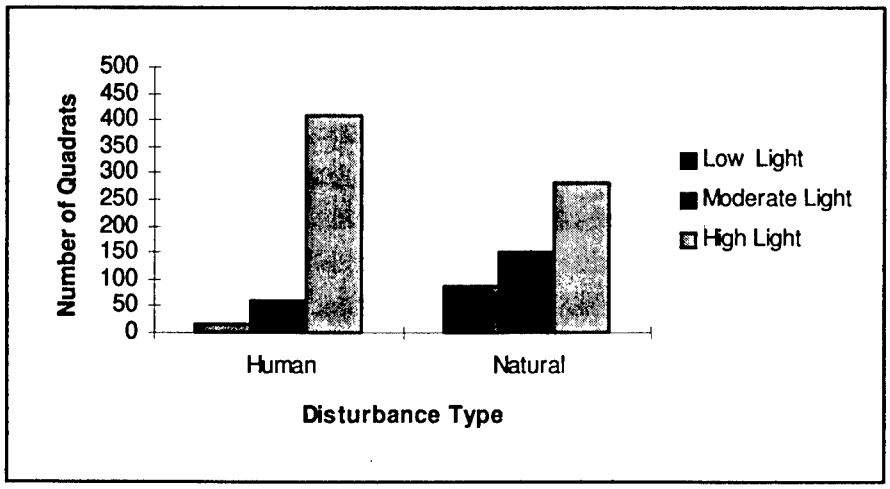
The most common disturbance type plus light level combination was human-high light level; 409 quadrats (41%). The least common was human-low light level; 14 quadrats (1%). The most common natural disturbance plus light level combination was natural-high light level; 281 quadrats (28%) (Figure 21 and Appendix E). A χ^2 test for independence for disturbance type by light level was significant (χ^2=110.531, p=0.001, df=2), meaning that the variables were dependent. The data suggest that human disturbance was more likely to result in a higher light level. Nonetheless, natural disturbance was also likely to result in a higher light level. Eight of the 27 populations (30%) were classified as natural-high light level, and 11 populations (41%) were classified as human-high light level. Population 3b had an equal number of natural-high light level and human-high light level quadrats.

Populations 2f, 5a, n4, n7, and n9 were dominated by quadrats classified as natural-moderate light level, while population n14 had more quadrats classified as human-moderate light level. Population 6 had a tie between quadrats classified as natural-low light level and natural-moderate light level (Appendix E). These seven populations should be monitored closely to ensure that the level of light reaching the herb layer does not become low enough to threaten population persistence. No interactions were tested between disturbance type and light level for the number of genets per quadrat or the number of inflorescences per quadrat.

Disturbance Degree and Light Level

The most common disturbance degree plus light level combination was low disturbance degree-high light level; 377 quadrats (38%). The least common was high disturbance degree-low light level; 4 quadrats (0.4%). The most common high degree disturbance plus light level combination was high disturbance-high light level; 175 quadrats (17%). The most common moderate degree disturbance plus light level combination was moderate disturbance-high light level; 138 quadrats (14%) (Figure 21 and Appendix E). A χ^2 test for independence for disturbance degree by light level was significant (χ^2=92.741, p=0.001, df=4), meaning that the variables were dependent. The data suggest that a low degree of disturbance was more likely





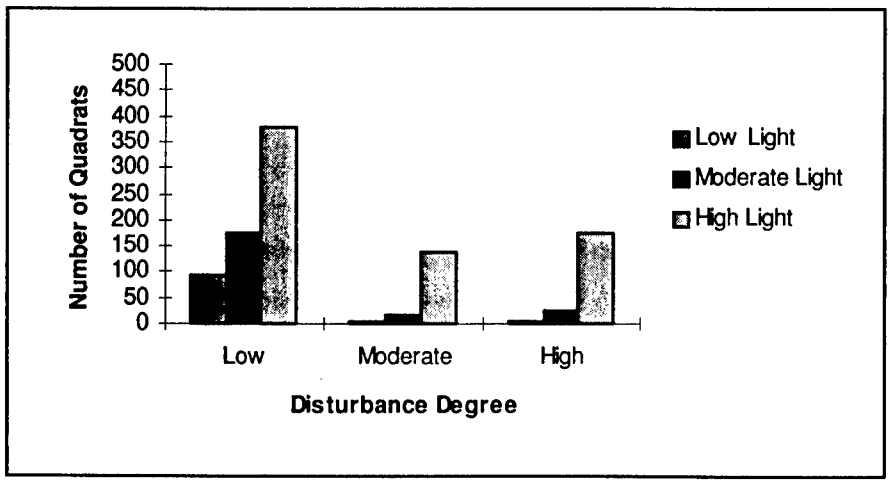


Figure 21. Overall number of quadrats per disturbance degree per disturbance type, overall number of quadrats per light level per disturbance type, and overall number of quadrats per light level per disturbance degree in 1996.

to result in a moderate or low level of light. Nonetheless, a high light level was most abundant in all disturbance degree classes. Fifteen of the 27 populations (56%) were classified as low disturbance-high light level. Populations 3b and n10 were classified as moderate disturbance-high light level. Populations 5a, n4, n7, and n11 were classified as low disturbance-moderate light level. Population n14 had a tie among quadrats classified as low disturbance-moderate light level, high disturbance-moderate light level, and high disturbance-high light level. Populations 3a, 4, and n10 were dominated by quadrats classified as high disturbance-high light level. Finally, populations 6 and n9 were dominated by quadrats classified as low disturbance-low light level. Which of these two variables, disturbance degree or light level, has a greater influence on population persistence is unknown. However, it is reasonable to believe that a high degree of disturbance (primarily human) may have an immediate and potentially irreversible impact on population persistence. That is, the habitat may be degraded to such a degree that the population can no longer maintain itself or is simply destroyed, preventing re-establishment. A low light level may have a gradual and reversible impact on population persistence. That is, once the canopy is thinned, e.g., by prescribed fire (mimic natural disturbance), the population may be able to rebound from the seed bank or migration. Populations 3a, 4, 6, n9, n10, and n14 should be monitored closely to ensure that the degree of disturbance does not become too severe, or the light level does not become too low to ensure population persistence. No interactions were tested between disturbance degree and light level for the number of genets per quadrat or the number of inflorescences per quadrat.

Disturbance Type and Disturbance Degree and Light Level

The most common disturbance degree plus disturbance type plus light level combination was natural, low disturbance-high light level; 260 quadrats (26%). There was a tie for the least common combination (with 0 quadrats) between natural, high disturbance-low light level and natural, moderate disturbance-moderate light level. The most common human disturbance plus disturbance degree plus light level combination was human, high disturbance-high light level; 172 quadrats (17%). Fourteen of the 27 populations (52%) were dominated by the most acceptable combinations of natural, low disturbance-high light level, and human, low disturbance-high light level. Nine populations (33%) were dominated by the acceptable combinations of human, moderate disturbance-high light level natural, low disturbance-moderate light level; and natural, low disturbance-low light level. Populations 3a, 4, and n2 were dominated by the relatively unsatisfactory combinations of human, high disturbance-high light level. Similarly, population n14 had a tie between the relatively unsatisfactory combinations of human, high disturbance-high light level, and human, high disturbance-moderate light level

(Appendix E). C. Helton (in prep) identified populations n1, n2, n5, n6, n12, n13, and n14 as populations of concern based on assessment of fire evidence, disturbance degree, general site quality, and population location. These seven populations in addition to populations 3a and 4 should be monitored closely to ensure that the degree of disturbance does not become so severe that it threatens population persistence. No interactions were tested among disturbance type, disturbance degree, and light level for the number of genets per quadrat or the number of inflorescences per quadrat.

Discriminant Analysis

In 1996, four vegetative and reproductive variables were selected to discriminate among the 26 populations (population n7 was removed because it had only one observation). Variables were (1) number of ramets per genet, (2) number of stems per genet, (3) number of inflorescences per genet, and (4) stem height per genet. Based on these variables simultaneously, little differentiation was detected among the populations. These results added support to the initial genetic variation tests conducted by Halward, Hill, and Shaw (in prep) which concluded that very little genetic variation existed within and among the five populations studied in 1995.

Principal Components Analysis

First, principal components analysis (PCA) was performed on standardized data using the correlation matrix (N=1002). The first two principal components explained 84.2% of the variation (57.5% and 26.7%, respectively) and had significant eigenvalues (>1.0) of 2.30 and 1.07, respectively (Table 13). The loadings for the first principal component revealed a strong significant correlation (0.610) with the number of stems per genet, although the loadings were also high for the number of

Table 13. Eigen values and component loadings from the principal components analysis in 1996.

Component	Eigenvalue*	Proportion Variance Explained	Ramet Loading	Stem Loading	Inflorescence Loading	Stem Height Loading
PRIN1	2.300	0.575	0.525	0.610	0.576	0.145
PRIN2	1.066	0.267	-0.325	-0.128	0.201	0.915
PRIN3	0.444	0.111	0.734	-0.201	-0.545	0.352
PRIN4	0.189	0.047	-0.283	0.756	-0.576	0.132

* Significant eigenvalues>1.0, significant loadings>0.162, α=0.01.

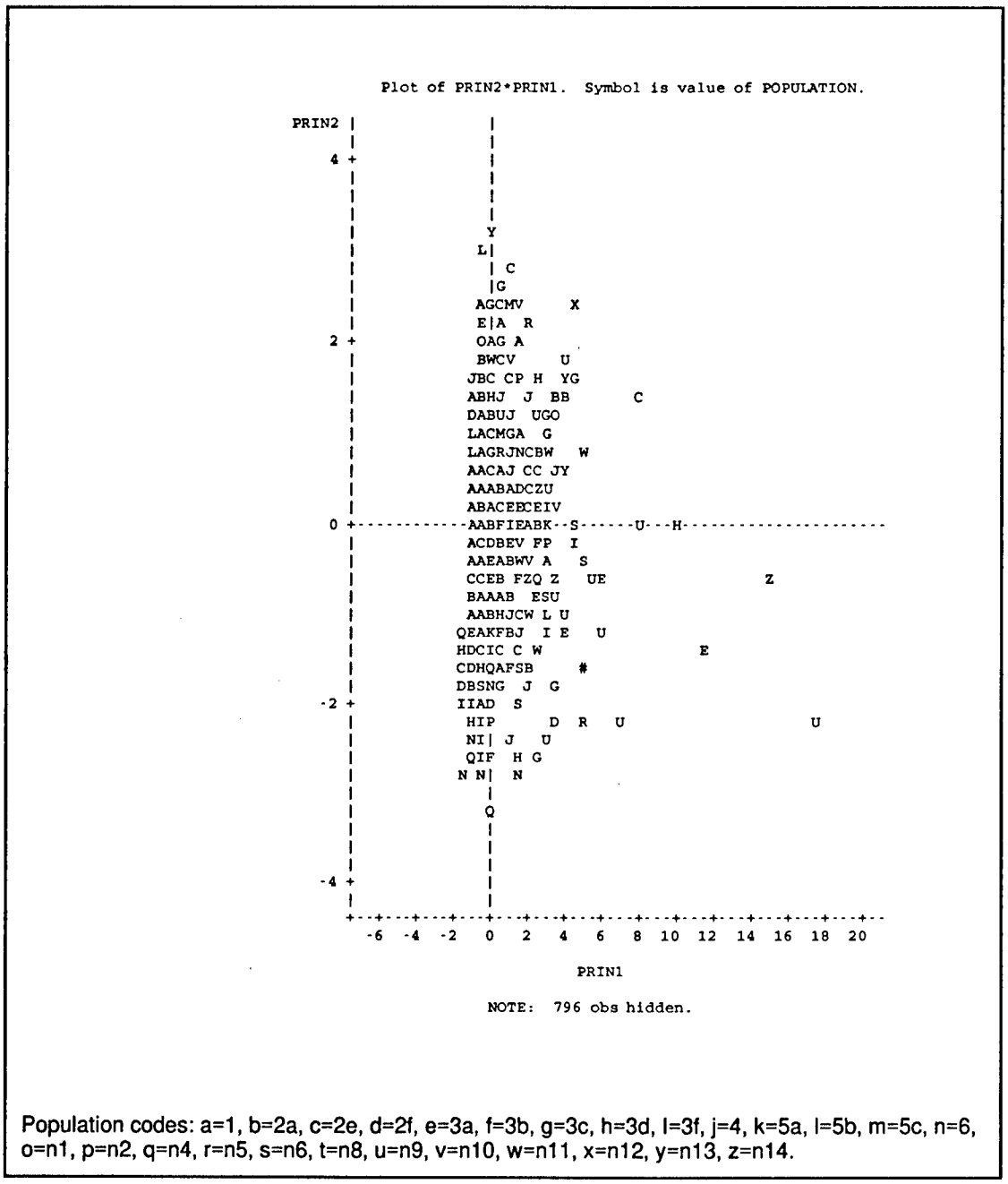
inflorescences per genet (0.576) and the number of ramets per genet (0.525). These three variables were correlated. The loadings on the second principal component revealed a strong significant correlation (0.915) with stem height per genet (Table 13). A plot of the second principal component scores by the first principal component scores revealed no separation of the populations based on these components (Figure 22). It also revealed no unique clustering of potential local ecotypes. Since the identity of the genetic populations was unknown, it was initially proposed that possibly identifying local ecotypes may provide insight into which populations were reproductively linked or isolated. This information would have been beneficial in determining more meaningful monitoring and management units, and in prioritization of populations for conservation. However, it did reveal that there was more variation explained by the first principal component, which was consistent with the eigenvalues.

Descriptive Discriminant Analysis

Next, descriptive (canonical) discriminant analysis (DDA) was performed on the four vegetative and reproductive variables from the 26 populations. First, a test was performed for within population covariance matrix homogeneity. Bartlett's test confirmed homogeneity at the 0.0001 level (χ^2=1,468, DF=250). However, this test is sensitive to a departure from normality. Consequently, a linear discrimination was performed. Linear discrimination is believed to be more stable with small sample sizes and nonnormality (Stevens 1996).

The univariate statistics (ANOVA) for the population means for each variable were significant (Table 14). Moreover, the multivariate statistic (MANOVA) criterion, Wilk's lambda (Λ), was 0.638 and significant at the 0.0001 level with an F-value of 4.64 (Table 14). That is, the population mean vectors for the four variables were not equal, which was consistent with the univariate results. However, an inverse relationship exists between Λ and the degree of separation among the populations. Moreover, tau squared (τ^2=1-$\Lambda^{1/r}$), which is a measure of the strength of association, was 0.106. These results imply that the degree of separation among the populations, although significant, was not substantial.

The first two canonical components (linear combinations) explained 70.9% of the variation (44.0% and 26.9%, respectively) and had significant eigenvalues of 0.212 and 0.130 (greater than the average eigenvalue of 0.121). Moreover, the squared canonical correlations revealed that the first canonical component had more discriminatory power (0.175) than the second canonical component (0.115) (Table 15).



Population codes: a=1, b=2a, c=2e, d=2f, e=3a, f=3b, g=3c, h=3d, I=3f, j=4, k=5a, l=5b, m=5c, n=6, o=n1, p=n2, q=n4, r=n5, s=n6, t=n8, u=n9, v=n10, w=n11, x=n12, y=n13, z=n14.

Figure 22. Plot of the second principal component scores by the firest principal component scores for all observations for each population in 1996.

The test of dimensionality on the canonical correlations were all significant (Table 16). That is, all four components may have been useful in representing any separation among the populations. Nonetheless, it was decided to examine the spatial separation of the populations in two dimensions using only the first two canonical components that explained most of the variation.

Table 14. Univariate and multivariate statistics from the descriptive discriminant analysis in 1996 (N=1002).

	F	Numerator DF	Denominator DF	P
Number of Ramets	3.37	25	976	0.0001
Number of Stems	5.28	25	976	0.0001
Number of Inflorescences	4.47	25	976	0.0001
Stem Height	7.11	25	976	0.0001
Wilk's Lambda (Λ)	4.64	100	3860	0.0001

Table 15. Eigen values and component loadings from the descriptive discriminant analysis in 1996.

Compo-nent	Squared Canonical Correlation	Eigenvalue*	Proportion Variance Explained	Ramet Loading	Stem Loading	Inflorescence Loading	Stem Height Loading
CAN1	0.175	0.212	0.440	0.059	0.257	0.123	0.858
CAN2	0.115	0.130	0.269	0.686	0.966	0.736	-0.171
CAN3	0.087	0.095	0.197	0.087	-0.007	0.648	0.485
CAN4	0.044	0.046	0.095	-0.720	0.023	0.153	0.019

* Significant eigenvalues >0.121, significant loadings >0.162, α=0.01

Table 16. Test of dimensionality on the canonical components (linear combinations) in 1996.

	Wilk's lambda (Λ)	F	Numerator DF	Denominator DF	P
CAN1	0.638	4.64	100	3860	0.0001
CAN2	0.773	3.64	72	2912	0.0001
CAN3	0.873	2.97	46	1950	0.0001
CAN4	0.956	2.03	22	976	0.0033

The loadings for the first canonical component revealed a significant correlation (0.858) with mean stem height per genet. The loadings on the second canonical component revealed a significant correlation (0.966) with the number of stems per genet, although the loadings were also high for the number of inflorescences per genet (0.736) and the number of ramets per genet (0.686) (Table 15). These three variables were correlated. These results paralleled those produced from the PCA.

Consecutive MANOVAs were performed, removing each outcome variable in turn and examining the resultant Wilk's lambda (Λ) value, to determine the variable that was most important in contributing to population separation. The variable that, when removed, resulted in the highest Λ value was the most important; the variable that, when removed, resulted in the second highest Λ value was the second most important, and so on. Average stem height per genet contributed the most to population separation (0.766) followed by a tie between the number of stems per genet (0.712) and the number of inflorescences per genet (0.712), with the number of ramets per genet (0.669) contributing the least (Table 17). Average stem height also strongly defined the first canonical component, which was responsible for explaining most of the variation. None of the tests resulted in a nonsignificant population separation.

The standardized raw canonical coefficients revealed that the populations differed most widely on the first linear function, -0.049×ramets + 0.798×stems + 0.076×height -0.296×inflorescences, and next on the second linear function, 0.028×ramets + 0.761×stems - 0.020×height + 0.080×inflorescences. However, a plot of the second canonical component scores by the first canonical component scores revealed no separation of the populations (Figure 23). Nonetheless, it did reveal that there was more variation explained by the first canonical component, which was consistent with the eigenvalues. Furthermore, a classification based on the linear discriminant function had a high error rate (0.87) meaning there was poor discrimination among the populations (Table 18). These results were consistent with the results of the principal components analysis.

Table 17. Wilk's lambda values from consecutive MANOVAs for determining which variable was most important in contributing to population separation in 1996.

Variable Removed	Λ	F	Numerator DF	Denominator DF	P
Stem Height	0.766	3.63	75	2913	0.0001
Number of Inflorescences	0.712	4.67	75	2913	0.0001
Number of Stems	0.712	4.67	75	2913	0.0001
Number of Ramets	0.669	5.60	75	2913	0.0001

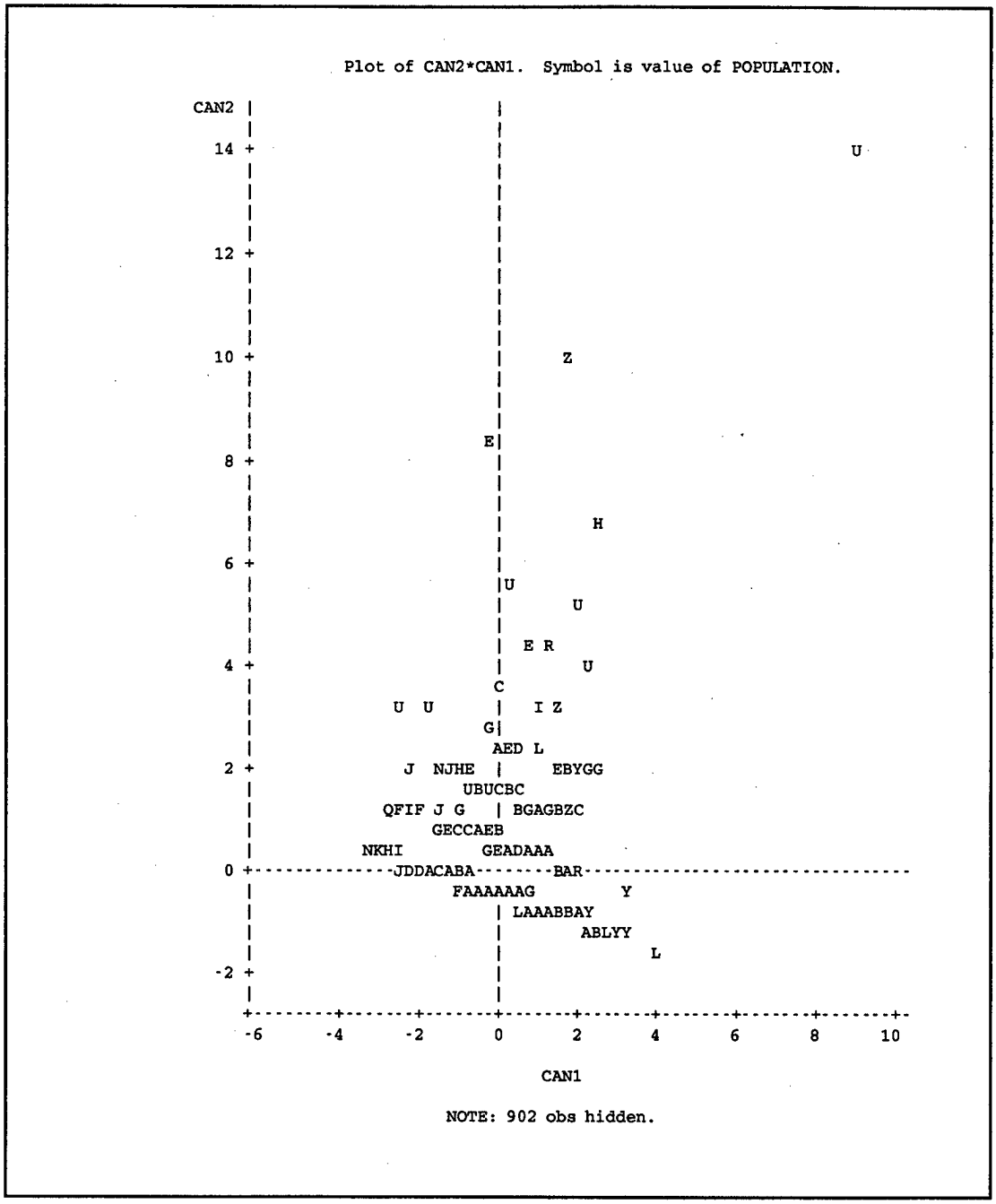


Figure 23. Plot of the second canonical component scores by the first canonical component scores for all observations for each population in 1996.

Figure 24 shows a plot using only the class means on the first and second canonical components for each population. The plot revealed that populations 6, n5, n9, and n14 were possibly more disparate from the other populations. These populations also had some of the lower classification error rates (0.28, 0.70, 0.79, and 0.80, respectively). Moreover, the results of the all possible pairwise comparisons (α=0.0325) revealed that populations 6, n9, and n14 were significantly different from many of the other populations (19, 22, and 20, respectively). Populations 3c, 4, 5b,

Table 18. Canonical discriminant classification error rates per population and overall in 1996 (prior probabilities equal 0.0385).

Population	Error Rate	Population	Error Rate	Population	Error Rate
1	1.00	4	0.74	n6	1.00
2a	1.00	5a	0.75	n8	1.00
2	0.90	5b	0.82	n9	0.79
2f	0.90	5c	0.92	n10	0.93
3a	0.98	6	0.28	n11	0.98
3b	0.96	n1	0.74	n12	1.00
3c	0.82	n2	0.98	n13	0.92
3d	1.00	n4	0.81	n14	0.80
3f	1.00	n5	0.70	Overall	0.87

and n13 were also significantly different from several other populations (11, 11, 10, and 14, respectively). All of the other populations, including population n5, were not significantly different from more than six other populations (Appendix F and Appendix G). These results collectively suggest that populations 6, n9, and n14 may be characteristically different from the other *B. atropurpurea* populations on Fort Stewart, based on these four variables. However, population n5 may not be characteristically unique from most of the other populations.

On the whole, these results appear to be marginal at best. Nonetheless, populations 6, n9, and n14 were somewhat isolated and may represent locally isolated reproductive units. These populations were not sampled in Halward, Hill, and Shaw's genetic variation study (in prep). Additional genetic screening will be required to clarify the biological uniqueness of any of the *B. atropurpurea* populations. This plant is an obligate outcrossing species with bees and butterflies as the suspected pollinators. Bees and butterflies are known to be potential long-distance pollen vectors (e.g., Schmitt 1980; Courtney, Hill, and Westerman 1982; Kwak et al. 1991; Rathcke and Jules 1993 and references therein). Since the *B. atropurpurea* populations are all within approximately 5 km of each other, it is reasonable to believe that pollen transfer among all the populations could have occurred in the past. This could partly explain the observed low level of among population genetic and morphological variation. It is also reasonable that since populations 6, n9, and n14 are small isolated populations they may have received less pollen input from outside populations over time. This may explain their slight differentiation from the other populations. Nonetheless, it is also reasonable that this species has always had a low level of genetic variation and the observed morphological variation was merely a plastic response to local environmental variation.

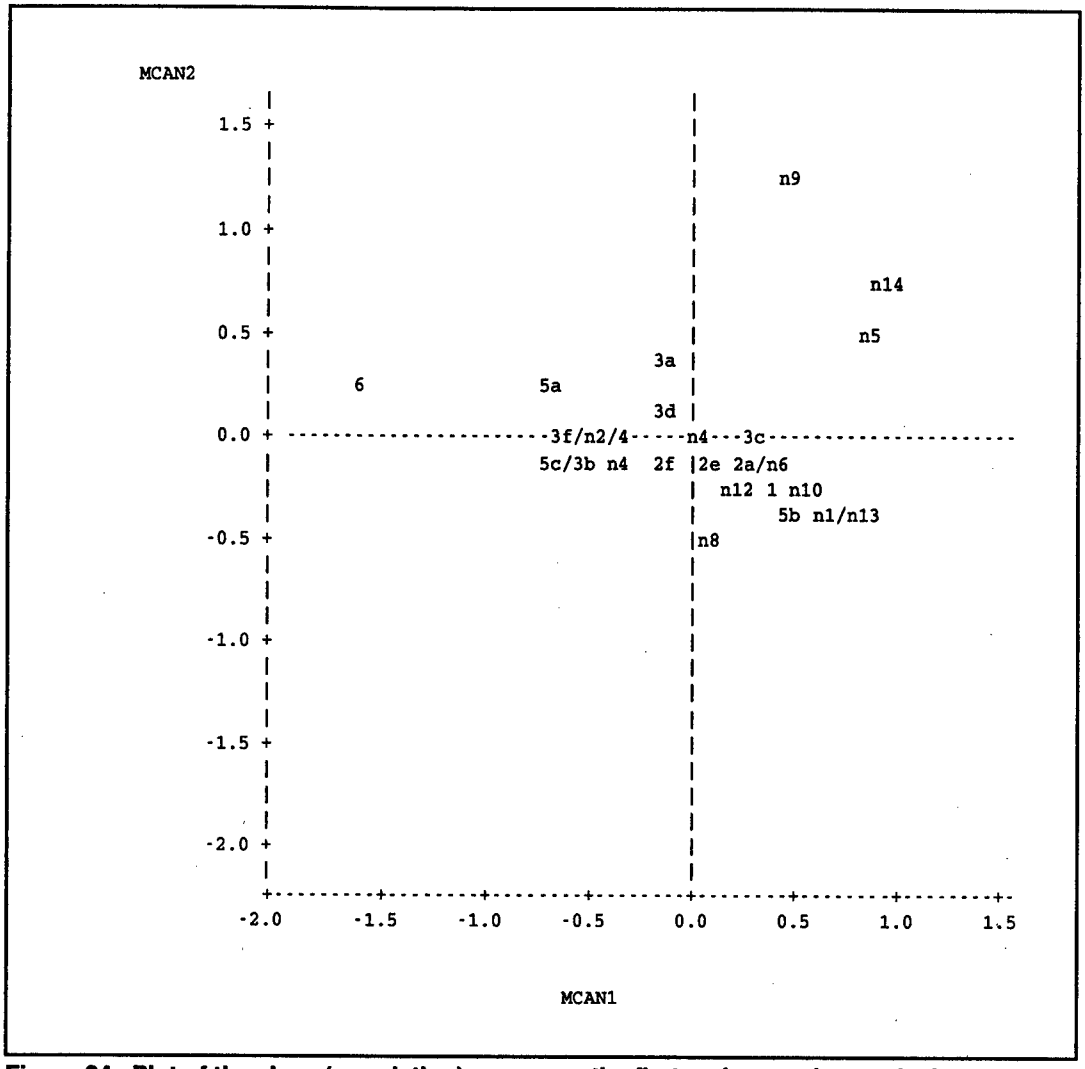


Figure 24. Plot of the class (population) means on the first and second canonical components in 1996.

5 Conclusions and Recommendations

Conclusions

Table 19 summarizes the principal questions addressed in this study and their respective results and conclusions. It provides a succinct overview of each project task area and often refers back to more detailed information in the previous chapters. The principal conclusions for each project task area are discussed below.

Table 20 provides a summary of the principal variable characterizations per population in 1996. (Some of this information was presented in figures in the main text; the numbers are presented here.) This table is meant to aid in distinguishing and understanding the differences among the populations. Table 20 and Appendix A provide a quick reference to the principal summary information on each *B. atropurpurea* population on Fort Stewart.

As of October 1996 there were 29 *B. atropurpurea* populations located and delineated on Fort Stewart. However, one of the populations discovered in 1995 (population n3) was not found again in 1996. The number of *B. atropurpurea* populations and the number of individuals occurring on Fort Stewart was much greater than initially assumed. It is now highly probable that Fort Stewart contains the greatest number of known populations and individuals of this species in the Southeast United States. The word 'population' does not refer to a population in the genetic sense, but refers only to a distinct physical occurrence of the species within the landscape (a study site). In 1996, there was an upper bound estimate of 44,299 genets, and a lower bound estimate of 10,477 genets on Fort Stewart. Because of difficulties in obtaining reliable density estimates, the true population size probably existed somewhere between these two estimates. Nonetheless, this appeared to be a substantially large population on Fort Stewart. Seven populations (populations 2a, 2e, 3c, 3d, n6, n12, and n13) were estimated to contain more than 1,000 genets; 15 populations (populations 2f, 3f, 5a, 5c, 6, n1, n2, n4, n5, n7, n8, n9, n10, n11, n14) were estimated to contain fewer than 100 genets. The populations encompassed a scattered area of 258,858 m^2 (25.9 ha) with only six populations (populations 2a, 2e, 3c, 3d, n6, and n12) larger than 10,000 m^2 (1 ha). The average population larger than 10,000 m^2 was 35,523 m^2 (3.55 ha), and the average population less than 10,000 m^2 was 2,177 m^2 (0.22 ha).

Table 19. Summary of the task area questions, results, and conclusions for the *B. atropurpurea* study at Fort Stewart in 1995 and 1996.

Task Area	Question	Results	Conclusions
Population Data	What is the location and physical extent of each population?	population map Figure 4, 29 populations, in 4 counties, 5 training areas, and 3 conservation sites, encompassing 25.9 ha, 6 populations > 1 ha Table 3	more populations than initially assumed, Fort Stewart may have greatest number of known populations, most populations small, and concentrated in open area
	On what soil types do the populations occur?	5 soil types: Ellebelle, Fuquay, Leefield, Osier, and Pelham	poorly drained, moderately permeable, loamy sands, low organic matter, acidic, and seasonally high water table
	What is the number of genets for each population (population size)?	population sizes in Table 3, overall population size between 10,477 - 44,299 genets, 7 populations > 1,000 genets	substantially large population at Fort Stewart, most populations small
	What is the density of the genets in each population?	avg. population densities in Figure 8, overall genet density ranged from 0.03 genets/m^2 - 3.0 genets/m^2	low density as expected for rare plant, difficult to accurately estimate
	Does the density of genets vary among populations?	yes	extremes may be due to varying sampling intensity
	What is the dispersion of genets in each population?	aggregated dispersion based on three calculated indices Table 6	aggregated dispersion as suspected, showed two levels of aggregation: patch scale and population scale
	Does the dispersion of genets vary among populations?	yes, 5a and n9 were randomly dispersed	aggregated and random dispersions may be result of dispersal patterns, patchy environment, or military disturbance
Vegetative Growth	What is the vegetative condition of flowering individuals in each population?	population means in Figures 9 & 10, overall stem height 72.86, 3 ramets, 2 stems per genet, 56% - 60% of ramets stemmed and flowering	overall vegetative health not threatened by predation or herbivory, genets composed of multiple ramets, nearly half of population inconspicuous, size class determination needs more study
	Do the vegetative characters vary among populations?	ramets and stems per genet relatively consistent, stem height highly variable	stem height may be responding to local environmental variation particularly light levels
Reproduction	What is the density of inflorescences in each population?	avg. population floral densities in Figure 11, overall floral density 0.3 inflorescences/m^2 - 7.3 inflorescences/m^2	similarly to genet density, floral density showed two levels of aggregation: patch scale and population scale
	Does the density of inflorescences vary among populations?	yes, highly variable	extremes may be due to varying sampling intensity, possibly response to local environmental variation
	What is the condition of floral production in each population?	avg. population floral production per genet in Figure 11, overall 3 - 4 inflorescences per genet, 3 inflorescences per ramet	floral production was variable among populations, typical ramets have multiple inflorescences, approximately 60% of genets and ramets were flowering
	Do floral characters vary among populations?	yes, highly variable	probably due to local environmental variation, more vigorous plants produced more inflorescences
	What is the seed production in each population?	avg. population seed production in Figure 12, overall 36 mature seeds per inflorescence, 30% seed set per inflorescence	low seed set, microlepidopteran predation potential problem
	Does seed production vary among populations?	yes	possibly due to local environmental variation (resource limitation) or population size (inbreeding depression)
	What proportion of the seed production is viable?	avg. population viability in Figures 14 & 15, overall 75% seedling emergence in the greenhouse, rapid initial emergence, avg. emergence rate 4 days	seed viability high, seedlings healthy, chlorotic seedlings possible sign of inbreeding depression
	Does the proportion of viable seeds vary among populations?	yes	possibly due to poor condition some of the seeds were collected, resource allocation tradeoff, or inbreeding depression

Table 19. (Continued.)

Task Area	Question	Results	Conclusions
Phenology	When is the beginning, peak, and completion of germination, rosette growth, stem elongation (bolting), flowering, seed dispersal and winter dormancy?	phenological time line in Figure 16	improved knowledge of phenology, need additional examination of seed dispersal, seed germination and winter dormancy
Environmental Data	What is the environmental condition of each population based on the frequency of disturbance type, disturbance degree and light level classes?	population characterizations in Appendix E, populations characterized by natural disturbance (67%), low disturbance degree (78%), and high relative light levels (78%)	most populations have acceptable habitat conditions, military ORV disturbance, and shrub and tree invasion potential problems
	Is there any relationship among disturbance type, disturbance degree and light level?	yes, human activity more likely to result in greater disturbance degree and higher relative light level, plus low disturbance degree more likely to result in moderate or low relative light levels	high relative light level was most common in both natural and human disturbance classes
	Does the density of genets and inflorescences differ among disturbance type, disturbance degree and light level classes?	disturbance type and light level classes - no, Figures 18 & 20, disturbance degree classes - yes, Figure 19	as long as disturbance degree not too severe may not make a difference whether it is natural or human disturbance, high disturbance may negatively impact genet density more than floral density
Discriminant Analysis	Are there simultaneous population mean differences (centroid separation) with respect to the number of ramets per genet, number of stems per genet, number of inflorescences per genet, and mean stem height per genet?	little or no differentiation among populations, Wilk's lambda 0.638, tau squared 0.106, and the discriminant classification error rate 0.87 all imply low degree of separation among populations	lack of differentiation adds support to initial low genetic variation finding, no local ecotypes evident, any differentiation may only be a plastic response to local environmental variation
	Can these differences be meaningfully characterized by some linear combination of the four variables?	yes, PCA component 1 (57.5%) and PCA component 2 (26.7%) explained 84.2% of the variation Table 13, and DDA component 1 (44.0%) and DDA component 2 (26.9%) explained 70.9 % of the variation Table 15	The first two PCA and DDA components could be used to examine the population mean differences in two-dimensional space
	Can the linear combination of variables be meaningfully defined?	yes, PCA component loadings in Table 13 and DDA component loadings in Table 15	PCA component 1 correlated to number of stems, number of inflorescences, and ramets, PCA component 2 correlated with stem height, DDA component 1 correlated with stem height, DDA component two correlated with number of stems
	Which of the four variables contributes most to the population mean differences?	average stem height, Table 18	avg. stem height explained most of the variation, stem height was also the most variable
	In how many dimensions can this population mean separation be represented?	2, the first two PCA and DDA components explained most of the variation and had significant eigenvalues	population mean separation examined in only these two dimensions revealing little separation
	What population separation configuration is produced by the population means?	Figure 24 shows plot of population means on first two DDA components	little or no differentiation among populations , although populations 6, n9, and n14 may be more disparate from the other populations

Table 20. Summary of the major variable characterizations for each task area per population in 1996.

Population	Area (m^2)	Genet Density / m^2	CI Density	Estimated Population Size	Disperson	Ramets / Genet	Stems / Genet	Height / Genet (cm)	Floral Density / m^2	Inflorescences / Genet	% Ramets Flowering	Disturbance Type (DT)	Disturbance Degree (DD)	Light Level (L)	DT + DD + L	DDA Classification Error Rate
1	2,202	0.44	0.09	969	Agg	2	1	76.26	0.5	3	58	Natural	Low	High	N-L-H	1.00
2a	80,03	0.04	0.02	3,201	Rand/	3	1	75.65	0.0	3	50	Natural	Low	High	N-L-H	1.00
2e	11,76	0.16	0.03	1,882	Agg	3	1	77.29	0.1	4	54	Nat/Hum	Low	High	N-L-H	0.90
2f	8,799	0.00	0.01	34	Agg	3	1	67.59	0.0	2	41	Natural	Low	Mod	N-L-M	0.90
3a	4,705	0.20	0.06	941	Agg	3	2	70.05	0.3	4	66	Human	High	High	H-H-H	0.98
3b	1,398	0.58	0.12	811	Agg	2	1	66.89	0.5	3	48	Natural	Low	High	N-L-H	0.96
3c	17,35	0.24	0.02	4,166	Agg	3	2	79.02	0.6	4	46	Natural	Low	High	N-L-H	0.82
3d	39,26	0.36	0.03	14,135	Agg	3	2	69.22	0.1	3	57	Natural	Low	High	N-L-H	1.00
3f	1,144	0.25	0.03	286	Rand/	3	1	65.39	0.1	2	50	Natural	Low	High	N-L-H	1.00
4	1,701	0.38	0.04	647	Rand/	2	1	70.89	0.7	4	70	Human	High	High	H-H-H	0.74
5a	96	0.67	0.11	64	Rand/	3	2	69.03	0.1	4	56	Natural	Low	Mod	N-L-M	0.75
5b	1,276	0.34	0.04	434	Agg	2	1	74.97	0.1	2	63	Natural	Low	High	N-L-L	0.82
5c	1,135	0.19	0.03	216	Agg	2	1	64.36	0.1	2	48	Human	Low	High	H-L-H	0.92
6	255	2.00	0.07	511	Agg	3	1	49.62	0.6	2	47	Natural	Low	Low	N-L-L/N-L-	0.28
n1	206	0.05	0.03	10	Rand/	2	1	81.36	0.0	2	65	Natural	Low	High	N-L-M/N-L-	0.74
n2	4,474	0.00	0.02	76	Agg	2	1	68.27	0.0	3	56	Human	High	High	H-H-H	0.98
n4	219	0.36	0.04	79	Agg	2	1	65.88	0.4	2	61	Natural	Low	Mod	N-L-M	0.81
n5	1,373	0.00	0.02	16	Agg	4	2	78.82	0.0	3	55	Natural	Low	High	N-L-H	0.70
n6	45,73	0.06	0.02	2,744	Agg	3	1	75.46	0.0	3	47	Human	Low	High	N-L-H	1.00
n7	79	0.00	0.00	3	Reg	11	5	66.90	0.0	9	45	Natural	Low	Mod	N-L-M	----
n8	2,616	0.08	0.02	209	Rand/	2	1	74.24	0.0	2	63	Human	Low	High	H-L-H	1.00
n9	3,201	0.02	0.01	64	Rand/	4	3	73.87	0.4	5	63	Natural	Low	High	N-L-L	0.79
n10	1,279	0.25	0.03	320	Rand/	2	1	78.48	0.4	3	74	Human	Mod	High	H-M-H	0.93
n11	6,489	0.00	0.01	84	Agg	3	1	74.89	0.0	3	50	Natural	Low	High	N-L-M	0.98
n12	18,98	0.56	0.04	10,630	Agg	2	1	74.87	0.2	2	52	Natural	Low	High	N-L-M	1.00
n13	1,850	0.94	0.03	1,740	Agg	2	1	80.61	0.9	2	77	Natural	Low	High	N-L-M	0.92
n14	1,209	0.20	0.03	242	Agg	4	3	79.73	0.1	4	68	Human	High	Mod	H-H-M/H-H-	0.80
More Info	Table 3	Figure 8	Figure 8	Table 3	Table 6	Figure 9	Figure 9	Figure 10	Figure 11	Figure 11	Table 9	Appendix E	Appendix E	Appendix E	Appendix E	Table 19

The genet density (0.30 genets/m^2) was particularly low as expected for a rare species. The three calculated measures of plant dispersion indicated an aggregated dispersion of individuals. Populations 2a, 3f, 4, 5a, n1, n8, n9, and n10 may have some characteristics of a random distribution of plants. The populations of this species were also aggregated at the landscape level within the wetland matrix and open range conditions found on Fort Stewart. These results and personal observations revealed the existence of multiple spatial scales of pattern associated with this species' distribution across the landscape. These different spatial scales should be considered in research, monitoring, and management projects. Depending on the scale of interest, improvements in the sampling strategy and/or sample size will be needed to more accurately estimate genet density for this species.

The vegetative condition and general health of the individuals was not severely threatened by disease or predation. Vegetative propagation was observed on several individuals as short, basal offshoots from the main rootstock. It is not known to what extent this serves as true vegetative reproduction. Vegetative reproduction did not appear to be a significant component of the life-history strategy for this species. Nonetheless, its existence makes the identification of single genetic individuals more difficult. Consequently, monitoring the flowering stems may be more easily accomplished and more useful for management purposes. The typical genet consisted of multiple ramets (3 ramets per genet) with over half of these ramets stemmed and flowering (2 stems per genet). Genets in populations n5, n7, n9, and n14 had a relatively greater number of ramets per genet while populations n8 and n13 had relatively fewer ramets per genet than all other populations. Populations n5, n7, n9, and n14 had a relatively greater number of stems per genet while population n8 had relatively fewer stems per genet than all other populations. No substantive meaning could be proposed for the relatively high or low means based on the characteristics of the populations. The mean stem height was 72.86 cm. Population 6 had a relatively low mean stem height compared to the other populations and was the only population characterized as having a low relative light level. Stem height was variable and may have been more responsive to the environmental conditions of each population. However, the environmental variable that was most responsible for influencing stem height was indiscernible. More research is needed to characterize the environmental condition of each population and its influence on vegetative and reproductive condition. This should include both biotic and abiotic components, such as species composition, species importance values, nearest neighbors, soil conditions, hydrologic conditions, light levels, disturbance, etc. More research is also needed to determine the characters that may be used to determine size classes for this species.

Floral production was variable among populations, seed production was low, and seed viability was high. Predation on floral structures and a fungus on the disk flowers was occasionally observed. Predispersal seed predation by lepidopteran larvae from the genus *Metznaria* was also observed in several seed samples from populations 1, 2, 4, and 5. Seed predation may be a potential problem. The typical ramet had three inflorescences in 1995 on average. The typical genet had 3 infloresences in 1995 and 4 inflorescences in 1996 on average. Populations 5a, n7, n9, and n14 had a relatively greater number of inflorescences per genet while populations 2f, 5b, and 5c had fewer inflorescences per genet than all other populations. No substantive meaning could be proposed for the high or low means based on the characteristics of the populations. There were 60% of the ramets flowering in 1995 and 56% of the ramets flowering in 1996. There were 61% of the genets flowering in 1995. Consequently, to the casual observer a significant portion of the population was relatively inconspicuous. Populations 2f, 3b, 3c, 5c, 6, n6, and n7 had a greater percentage of ramets in the vegetative stage. No substantive meaning could be proposed for the greater percentage of ramets remaining in the vegetative state. Populations 2a, 3f, and n11 had an equal percentage of flowering and vegetative ramets. The mean inflorescence density was 7.3 inflorescences/m^2 in 1995 and 0.3 inflorescences/m^2 in 1996. Mean floral density was variable. Depending on the scale of interest, improvements in the sampling strategy and/or sample size will be needed to more accurately estimate floral density for this species.

Table 21 provides a summary of the major reproduction variable characterizations per population in 1995. Some of this information was presented as figures in the main text but the actual numbers are presented here. This table is meant to aid in distinguishing and understanding the differences among the populations discussed in the text. It provides a succinct overview of each variable characterization for each population and, where possible, refers back to more detailed information in the main text.

Table 21. Summary of the major reproduction variable characterizations per population in 1995.

Population	Inflorescences / Genet	Inflorescences / Ramet	Number of Ray Flowers	Capitulum Width (cm)	Total Ovule Number	Mature Seed Number	Seed Set	Total Mature Seed	Mean Mature Seed	Proportion Seedling	Seedling Emergence Rate
1	6	3	16	2.14	155	25	0.15	28.70	1.20	0.97	3
2	5	3	15	2.15	140	34	0.25	45.80	1.30	0.82	4
3	4	3	14	2.12	124	54	0.48	54.20	1.00	0.71	5
4	3	3	15	2.09	105	24	0.22	32.40	1.30	0.81	3
5	3	2	14	2.00	142	18	0.12	22.20	1.20	0.46	4
More	Table 8	Table 8	Table 10	Table 10	Fig 12	Fig	Fig	Fig 13	Fig 13	Fig 14	Table 11

Based on the 33 seed samples collected in 1995, there were 127 ovules per inflorescence on average, but only 36 seeds per inflorescence were mature on average. Seed production was variable among populations. The seed set of 30% was relatively low compared to other rare composites. The low seed set implied that a considerable number of seeds were possibly aborted or never filled. The low seed set may have been the result of resource limitation or lack of pollination. Seed mass was also variable among populations. The overall mean mature seed mass per inflorescence was 41.2 mg with a mean individual mature seed mass of 1.2 mg. Population 3 had a relatively low mean individual mature seed mass compared to the other populations. This population also had a greater number of mature seeds per infloresence than the other populations on average. It is reasonable that the lower individual seed mass represents a tradeoff between seed number and seed mass. The mean individual mature seed mass was relatively small compared to other composites, but may be considered a medium sized seed.

The seed viability test indicated that seed viability was high and that seedlings were healthy. Mold was observed on some seedlings, and others lacked chlorophyll or had three cotyledons. Once removed from the cold stratification, no seedling emergence in the greenhouse was observed until the second day. Initial seedling emergence was relatively rapid and peaked on day 4 with 17% of the seedlings emerging. Population 4 peaked on day 2 with 31% of the seedlings emerging, and population 5 had the latest and lowest peak on day 5 with 11% of the seedlings emerging. No substantive meaning could be proposed for the population differences. The overall rate of seedling emergence (T50) was most rapid between days 2 and 5 with 50% of the seedlings emerging on average by day 4. Population 3 which had the largest mean number of mature seeds and the lowest mean individual mature seed mass also had the slowest seedling emergence rate. The overall pattern of seedling emergence was comparable to those of other plant species. The mean proportion of seedling emergence in the greenhouse on day 14 was 75% and was relatively high compared to other composites. The relatively low percentage of seedling emergence observed in population 5 may have been due to the wet conditions in which the seeds were collected and shipped back to Illinois. It was in this population where rotten seeds and the germination of seeds in the heads upon arrival in Illinois was observed. Flower pollination, seed dispersal, seed dormancy, post dispersal seed predation, and seedling establishment were not assessed. Study of these aspects of sexual reproduction may be of value in advancing an understanding of the breeding system and life-history strategy of *B. atropurpurea*. Furthermore, seed viability may have to be checked for the populations discovered by C. Helton and all future populations.

Based on field observations in 1995 and 1996, a phenological time line for major, seasonal life-history events was constructed. Rosette growth was believed to occur primarily during the growing season from mid-March to late October. Stem elongation, or bolting, began in early to mid-June and continued through September. Flowering was initiated in mid-August, peaked in mid-September, and continued into early October. Seed dispersal was believed to have begun late in the flowering period for early flowering individuals, but probably occurred mostly during the late fall and into the following spring. Much of the data on the vegetative and reproductive condition of *B. atropurpurea* suggested that this species' life-history strategy was consistent with a plant inhabiting mid-successional habitats.

The qualitative assessment of the environmental condition of the *B. atropurpurea* populations characterized the populations as having been influenced by natural disturbance (52% of quadrats), having a low degree of disturbance (64% of quadrats), and having a high relative light level (69% of quadrats) overall. Sixty-seven percent of the populations were dominated by quadrats characterized by natural disturbance and 78% of the populations were dominated by quadrats characterized by a low degree of disturbance and quadrats characterized by a high relative light level. In relation to site quality, the main concern was for populations with a high degree of disturbance and/or low relative light level. Disturbance type was categorized as natural or human, and disturbance degree as low, medium, or high. Natural disturbance primarily referred to fire, animal disturbance, and other natural events. Human disturbance primarily referred to military ORV traffic, RCW cavity tree management, road maintenance, bivouac sites, foot traffic, extractive land uses, and other human activities. Low disturbance degree was characterized by little or no physical signs of alteration, moderate disturbance degree by some physical signs of alteration but not too severe, and high disturbance degree by severe physical signs of alteration to the soil or vegetation. Light level was categorized as low (shaded), moderate (part sun), or high (full sun). Low light level was characterized by a significant degree of shading, moderate light level by some degree of shading but not too significant, and high light level by little or no degree of shading at or near the ground surface. There was nearly an even number of quadrats characterized as having natural or human disturbance. This suggested that human disturbance, primarily military ORV traffic, may be a significant threat to the integrity of *B. atropurpurea* populations. However, a comparison of genet density and floral density between natural and human disturbance classes suggested that as long as the disturbance was not too severe it may not make a difference to the persistence of *B. atropurpurea* populations whether the disturbance was natural or human. Nonetheless, the data suggested that human activity was more likely to result in a greater degree of disturbance. Populations 3a, 4, 5c, n2, n6, n8, n10, and n14 were dominated by quadrats classified as human disturbance. Based on the same

comparisons among disturbance degree levels, the results suggested that a high degree of disturbance may have a negative effect on the number of individuals present in a population, but not necessarily on the number of inflorescences produced in a population. Population n10 had slightly more quadrats classified as moderate disturbance. Populations 3a, 4, n2, and n14 were dominated by quadrats classified as high disturbance. C. Helton (in prep) only reported a high level of disturbance in populations n2, n3 (which was not found again in 1996), n6, and n11. It is believed that population n3 may have been eliminated due to severe ORV traffic. The relatively low light levels found in populations 2f, 5a, 6, n4, n7, and n14 were primarily due to shrub and tree invasion and may be improved with the use of prescribed burns. No significant results were found for the same comparisons among the light levels, although the data suggested that high light conditions were more conducive to greater floral production. More study is needed to determine the exact effects various human disturbances, degrees of disturbance, and levels of light may have on population persistence over time. The data also suggested that human disturbance (and natural disturbance to a lesser degree) was likely to result in a higher light level. Furthermore, a high disturbance degree was likely to result in a high light level, although a high light level was most abundant in all disturbance degree levels. Which of these two variables, disturbance degree or light level, has a greater influence on population persistence is unknown. Populations 3a, 4, n2, and n14 were dominated by quadrats characterized by the relatively poor combinations of human disturbance, high disturbance degree, and moderate or high light level combinations. These populations in particular should be monitored closely to ensure that human disturbance does not become too severe to threaten population persistence. C. Helton (in prep) identified populations n1, n2, n5, n6, n12, n13, and n14 as populations of concern based on assessment of fire evidence, disturbance degree, general site quality, and site location. These populations should also be monitored closely.

The principal components analysis and descriptive discriminant analysis using the number of ramets per genet, number of stems per genet, number of inflorescences per genet, and stem height per genet revealed little or no differentiation among the populations and no unique local ecotypes in 1996. These results added support to the initial genetic variation tests conducted by Halward, Hill, and Shaw that concluded very little genetic variation existed within and among the five populations studied in 1995. In the PCA, 84.2% of the variation was explained by the first two components, and in the DDA, 70.9% of the variation was explained by the first two components. Plots of the first two components against each other revealed little separation among the populations. Wilk's lambda (0.638) was large, and tau squared was low (0.106) which implied that the degree of separation among the populations was not substantial. Furthermore, the overall classification error rate

was high (0.87). Nonetheless, a plot of the population means from the DDA revealed that populations 6, n9, and n14 were possibly more disparate from the other populations based on these four variables. These populations also had some of the lower classification error rates (0.28, 0.79, and 0.80, respectively). Moreover, the results of the all possible pairwise comparisons revealed that populations 6, n9, and n14 were significantly different from many of the other populations. Additional genetic screening will be needed to clarify the biological uniqueness of any of the *B. atropurpurea* populations. It is reasonable that this species has always had a low level of genetic variation and that the observed morphological variation was merely a plastic response to local environmental variation.

Recommendations

The results of this project, and the recent work of C. Helton and Halward, Hill, and Shaw on *B. atropurpurea* have provided a foundation of understanding to build upon. Most importantly, they have identified the gaps in our knowledge base and have provided baseline information that natural resource managers may now use to plan future studies and management strategies. It is hoped that this information will assist natural resource managers at Fort Stewart, and across the Southeast, in streamlining future research and management programs.

As discussed in the Introduction, a basic understanding of species biology and ecology is necessary for developing management plans for species conservation. Furthermore, a systematic approach that can provide the necessary information to make the appropriate management decisions and progress assessments in a timely and cost-effective manner is needed. Such an approach is the TES conservation management approach outlined in Figure 1 that included demographic trend analysis, factor resolution, management, and assessment. Using the baseline information now available, a monitoring program may be more appropriately planned for *B. atropurpurea*. It is recommended that most *in situ* research and all management activities be incorporated into a monitoring program.

Before a monitoring program is established it is recommended that the *B. atropurpurea* populations and associated wetland habitats be given as much protection as possible from military ORV training and testing. Ultimately, the level of protection awarded each population will be contingent upon the natural resource manager's decision and negotiations with military trainers. The management guidelines for wetland communities, including inclusional wetlands, savannas, and sandhill seeps, provided by Trame and Harper (1997) and Harper and Trame (Draft) should be consulted to aid in these decisions. If adequate protection from ORV

traffic can not be obtained, then the guidelines outlined in Trame and Harper (1997) and Harper and Trame (Draft) for reducing the effects of ORV traffic on wetland communities should be considered. Since the effects of various military training and testing activities on TES species and plant communities are mostly unknown, unprotected populations may be used as research populations to help answer questions related to military impact. Several examples of these types of questions are offered by Trame and Harper (1997). *B. atropurpurea* populations should also be protected from other potential disturbances such as RCW management (e.g., cavity tree protection, brush clearing, fuel removal and raking, fire line construction, etc.), extractive land uses, road construction or maintenance activities, and ditching or draining. These activities, if unable to be prevented, may also provide opportunities for impact-related research.

Whether or not population protection ultimately can be achieved, a monitoring program for all populations should be planned and implemented. It is only through studying the demographic trends of individuals and populations that the limiting stage(s) of the life cycle can be identified, and the effects of management prescriptions or disturbances can be assessed. Once the stage of the life cycle that is limiting population growth or stability is identified, specific research may be conducted to determine what factors are limiting that stage's performance. Management prescriptions that may help mitigate this poor performance can be identified using the results of such research.

Annual demographic monitoring can be a resource intensive commitment. It requires thorough planning, years of data collection, solid statistical analysis, and consistent monetary support. Consequently, it is often difficult to implement for most species of concern. However, Menges and Gordon (1996) have outlined a three-level, hierarchical approach to rare plant monitoring that provides a flexible, rigorous, and feasible framework. This approach may be applied to *B. atropurpurea* at Fort Stewart. It is a nested approach where only a few populations receive intensive monitoring, but all populations receive a lower intensity of monitoring. The level of monitoring intensity provided each population depends on such factors as the degree of threat, local rarity, logistical constraints, prior data availability, and other management considerations. Table 22 summarizes one possible application of this three-level monitoring scheme to *B. atropurpurea* populations at Fort Stewart.

Level 1 monitoring involves observation of the species occurrence through annual assessment of the presence/absence or extent of each population. It may also

Table 22. An application of the three-level monitoring scheme to the B. atropurpurea populations at Fort Stewart.

Monitoring Level	Unit of Analysis	Purpose	Goal	Potential Populations
1	Occurrence or Location	Track Population Presence or Absence	Observe Trends Across Populations	All Populations
2	Population	Track Population Size and Condition	Observe Trends Within Populations	2f, 3a, 4, 5a, 5b, 5c, 6, n1, n2, n4, n5, n6, n7, n8, n9, n10, n11, n14
3	Individual	Demographic Monitoring of Individuals	Observe Individual Trends and Understand Demographic Mechanisms	Control Populations 1, 2a, 3c, n12, n13 and Treatment Populations Impacted by Disturbance, Fire, or Low Light

include more detailed information on the presence/absence of individuals in different size classes, estimated number of individuals, and qualitative assessment of surrounding land uses, disturbance events, and management treatments. Level 1 monitoring is meant to provide an early warning system for large changes in population health (Menges and Gordon 1996). At a minimum, this level of monitoring should be implemented for all *B. atropurpurea* populations at Fort Stewart.

Level 2 monitoring involves a more quantitative annual assessment of plant abundance or population size, site condition, and/or structure. Data on the reproductive status of the individuals should also be obtained. Level 2 monitoring provides an overall assessment of the population status, but does not identify size class specific trends or performance levels. This type of data is often collected from plots, transects, grids, quadrats, or other marked areas. It also requires reliable estimates of plant density (Menges and Gordon 1996). Obtaining a reliable estimate of plant density for *B. atropurpurea* was problematic. Consequently, suggestions for sampling designs and parameter estimations found in Travis and Sutter (1986), Owen and Rosentreter (1992), and Menges and Gordon (1996 and references therein) should be considered during the planning stage to help improve density estimation and ensure proper sampling design. This level of monitoring should be implemented for all *B. atropurpurea* populations at Fort Stewart. However, if current resources do not permit this level of monitoring, then those populations that are under the greatest threat or will be receiving direct management prescriptions should receive higher priority. Those populations that do not receive Level 2 monitoring should receive Level 1 monitoring. Populations that would be good candidates for Level 2 monitoring include 2f, 3a, 4, 5a, 5b, 5c, 6, n1, n2, n4, n5, n6, n7, n8, n10, n11, and n14. Most of these populations were characterized by low light

levels, high degrees of disturbance and/or small population size; therefore, they may be considered at greater risk.

Level 3 monitoring involves the intensive demographic monitoring of individuals through time. This level provides an assessment of the individual and population vital rates. Individuals are generally grouped into size classes, marked, and followed annually. This level of monitoring also follows nonflowering individuals, including seedlings that may be less conspicuous. This information may be used in population modeling and PVA (Menges and Gordon 1996). This level of monitoring is parallel to that discussed in the Introduction; therefore, refer back to that section and Lincicome (1998) for additional details. The characters that may best indicate size in *B. atropurpurea* needs further examination. This will be necessary before Level 3 monitoring can be implemented. Similar to Level 2 monitoring, Level 3 monitoring is also accomplished with the use of plots, transects, grids, quadrats, or other marked areas. Furthermore, reliable density estimates are also necessary; therefore, the same suggestions proposed above in Level 2 monitoring apply here. Level 3 monitoring is most appropriate for those species at greatest risk of extinction (Menges and Gordon 1996). Since *B. atropurpurea* is a former federally C2 listed species, insufficient data on the biological vulnerability of this species throughout its range exists to warrant listing as endangered or threatened, although such a listing may be appropriate. Therefore, full implementation of Level 3 monitoring is probably unwarranted at this time. Nonetheless, limited implementation of this monitoring intensity in certain populations in conjunction with Level 1 and/or Level 2 monitoring may serve as a highly valuable tool to better understand the population dynamics of this species and to assess the effects of management prescriptions and/or disturbance. Levels 1, 2, and 3 monitoring may also be nested within a population allowing greater flexibility and rapid management response with the least resource commitment (Menges and Gordon 1996). Level 3 monitoring should be planned for populations that are protected from disturbance and in good health, populations that are impacted by ORV disturbance, and populations that will receive unique management prescriptions. Potential control populations may be 1, 2a, 3c, n12, and n13. Populations that may be highly disturbed by ORV traffic may include populations 3a, 4, n2, n6, n11, and n14. The actual selection of control and treatment populations based on the future conditions of the *B. atropurpurea* populations is left up to the natural resource manager. The comparison of vital rates among control and disturbed populations, as well as, between control populations and populations influenced by various degrees or types of management prescriptions may provide valuable management information. The experimental design and replication of experimental units will be important considerations in this scenario (Travis and Sutter 1986; Menges and Gordon 1996 and references therein).

In addition to monitoring, several aspects of *B. atropurpurea*'s biology and ecology were identified as knowledge gaps. Additional research on these topics would be beneficial to the overall understanding of *B. atropurpurea* and may be required as a component of factor resolution if associated with a critical life-history stage. These topics would be best addressed as resources permit. Table 23 summarizes these additional research topics in no particular order of importance. It is left up to the natural resource manager or researcher to determine the topics that will need to be addressed as time goes by and opportunities arise.

Habitat characterization may be required to quantify the habitat conditions best suited for *B. atropurpurea*. This should include both biotic and abiotic parameters. Biotic parameters may include species composition, nearest neighbor associations, species importance values, vegetation structure, presence of soil microorganisms, etc. Abiotic parameters may include light levels, soil characteristics, hydrology, fire, etc. Many of the biotic and abiotic parameters may be included as components of the monitoring program. Research on the effects of various light levels, soil moisture levels, ORV disturbance levels, and fire levels on plant growth and reproduction are needed. In relation to disturbance and fire, the effects of different intensities, durations, frequencies, and seasonal timing of these events on plant growth and reproduction are also needed. Once again, experiments quantifying the effects of disturbance and fire may be best incorporated into the monitoring program.

Table 23. Additional research topics on *B. atropurpurea's* biology and ecology.

• Habitat Characterization Based on Biotic and Abiotic Parameters
• Effects of Different Light Levels on the Growth Rate and Reproductive Output
• Effects of Different Soil Moisture Levels on the Growth Rate and Reproductive Output
• Effects of Different Fire Regimes on the Growth Rate and Reproductive Output
• Effects of Different Levels of ORV Disturbance on the Growth Rate and Reproductive Output
• Pollination Biology
• Seed Ecology
• Seed Germination and Seedling Establishment
• Genetic Variation Within and Among All Known Populations
• Vegetative and Reproductive Phenology
• Extent and Importance of Vegetative Reproduction
• Quantification of Predation on Vegetative Structures and Seeds

Several aspects of sexual reproduction require further examination. Clarification of the pollination biology, including the identification of pollinators, the spatial extent of outcrossing, and the self-incompatibility mechanism, would aid in understanding the dynamics of reproduction and the genetic composition of this species. Furthermore, an examination of seed dispersal, seed dormancy, seed bank, and seedling establishment would all be useful in better understanding the life-history strategy and population dynamics of this species. A clarification of all aspects of reproduction would benefit the interpretation of monitoring results and research on the effects of disturbance and fire on population dynamics. Reproduction and establishment are key stages of the life cycle and any increase in the knowledge of these processes would benefit natural resource managers and conservation biologists in making better management decisions.

The assessment of genetic variation within and among populations should be expanded to include the populations discovered since Halward, Hill, and Shaw's study on the populations known prior to 1995. It may be beneficial to include *B. atropurpurea* populations outside of Fort Stewart for comparison. The three closest extant populations known to this author include the GNHP EO 33 near Manassas, EO 40 near Statesboro, and EO 9 near Snipesville.

Clarification of the seasonal phenology of this species would benefit natural resource managers in developing and timing management prescriptions. Phenological stages that require more detailed examination include initiation of winter dormancy, initiation of spring regrowth, initiation of bolting, seed dispersal, seed germination, and seedling establishment. These parameters may be included as components of the monitoring program.

Additional examination of the extent and role of vegetative propagation would also be beneficial. This information would be useful in understanding the life-history strategy and population dynamics of this species. This may be incorporated into the monitoring program.

Finally, the quantification of predation levels on both vegetative structures and seeds may be necessary. The identification of any predators and/or pathogens would also be beneficial.

In summary, the first priority should be to acquire as much protection as possible from military ORV disturbance for each *B. atropurpurea* population. Second, one of the three levels of monitoring should be planned and implemented for each population as soon as possible. This may require some additional preliminary estimation of plant density and plant size characterization. Third, once the

monitoring program has been established, fire should be restored to these populations as soon as possible. To prioritize each population in the overall burn plan, each population should be reassessed for the need of prescribed fire, the complete burn history for each population should be reviewed if available, and the possibility of incorporating a population into the RCW management regime should be assessed. As much documentation as possible on the fire conditions should be recorded in order to more meaningfully interpret any response in growth and reproduction. Fourth, as the need and/or resources permit the habitat characterization, pollination biology, seed dispersal, seed bank, seed dormancy, seedling establishment, genetic variation, phenology, vegetative reproduction, and predation research should be conducted. As the monitoring and research programs progress other research questions will arise and require consideration along with those left unanswered. Consequently, the importance of each of the above topics will always require adjustment in order to stay in line with changing landscape conditions and management goals.

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Abbreviations and Acronyms

ANOVA	Analysis of Variance
AR	U.S. Army Regulation
CEMML	Center for Ecological Management of Military Lands
CI	Closest Individual (Calculated Density)
C2	USFWS Level 2 Candidate Species
DA	U.S. Department of the Army
DDA	Descriptive Discriminant Analysis
DNA	Deoxyribonucleic Acid
DoD	U.S. Department of Defense
EO	Element of Occurrence
ESA	U.S. Endangered Species Act
FORSCOM	U.S. Army Forces Command
GIS	Geographic Information System
GPS	Global Positioning System
GNHP	Georgia Natural Heritage Program
GRASS	Geographic Resources Analysis Support System
G2	Natural Heritage Inventory Global Rarity Rank 2
G3	Natural Heritage Inventory Global Rarity Rank 3
HMU	Habitat Management Unit
I	Coefficient of Dispersion
I_E	Eberhardt's Index of Dispersion
I_P	Standardized Morisita's Index of Dispersion
Λ	Wilk's Lambda Multivariate Statistic Criterion
MANOVA	Multivariate Analysis of Variance
NRC	National Research Council
ORV	Off-Road Vehicle
PCA	Principal Component Analysis
PDA	Predictive Discriminant Analysis
PVA	Population Viability Analysis
RAPD	Randomly Amplified Polymorphic DNA
RCW	Red Cockaded Woodpecker (*Picoides borealis*)
SE	Standard Error of the Mean
SERDP	Strategic Environmental Research and Development Program
τ^2	Tau-squared Index of Association
TES	Threatened, Endangered and Sensitive Species

TNC	The Nature Conservancy
USACERL	U.S. Army Construction Engineering Research Laboratories
USDA SCS	U.S. Department of Agriculture Soil Conservation Service
USFWS	U.S. Fish and Wildlife Service
X^2	Chi-squared Statistic

APPENDIX A:

Summary of Location, Elevation, Soil Type, Habitat Type and Burn History Information for the *B. Atropurpurea* Populations at Fort Stewart

Summary of geographic location information including counties, USGS and NWI quadrangles, Fort Stewart training areas, and Fort Stewart conservation sites for the *B. atropurpurea* populations at Fort Stewart. Also summary information for elevation (*from Helton in prep), soil type, habitat type, and potential burn history (w=winter, s=summer) for the *B. atropurpurea* populations at Fort Stewart.

Population	TNC Element of Occurrence Number	County	USGS & NWI Quadrangle	Training Area	Conservation Site	Elevation (m)*	Soil Type	Habitat Type	Potential Burn History
1	702	Liberty	Glisson's Millpond	Echo 10	Sandhill Cemetery	32	Pelham	Pine / Cypress Savanna	w95
2a	706	Liberty	Glisson's Millpond	Echo 10	Sandhill Cemetery	32	Pelham / Ellabelle	Pine / Cypress Savanna	w94 s95
2e	706	Liberty	Glisson's Millpond	Echo 10	Sandhill Cemetery	32	Pelham / Ellabelle	Pine / Cypress Savanna	w90 w92 w95 s95
2f	706	Liberty	Glisson's Millpond	Echo 10	Sandhill Cemetery	32	Pelham	Cypress Dome / Savanna	w90 w92 w95
3a	703	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	32	Pelham	Pine / Cypress Savanna	w90 w95
3b	703	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	32	Pelham	Pine / Cypress Savanna	w90 w95
3c	703	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	32	Pelham	Pine / Cypress Savanna	w90 w95
3d	703	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	32	Pelham	Pine / Cypress Savanna	w90 w95
3f	703	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	32	Pelham	Pine / Cypress Savanna	w90 w95
4	701	Long	Glisson's Millpond	Echo 11	West of Sandhill Cemetery	10	Pelham	Shrub / Graminoid Wetland	w90
5a	704	Tattnal	Glisson's Millpond	Echo 19	North of Metz Pond Pinelands	50	Osier / Fuquay	Sandhill Seep / Wooded Stream Head	w90 w93 w95
5b	704	Tattnal	Glisson's Millpond	Echo 19	North of Metz Pond Pinelands	50	Pelham	Sandhill Seep / Wooded Stream	w90 w93 w95
5c	704	Tattnal	Glisson's Millpond	Echo 19	North of Metz Pond Pinelands	50	Pelham / Osier	Sandhill Seep	w90 w93 w95
6	705	Long	Glisson's Millpond	Echo 16	North of Long County Point	45	Pelham	Pine Woodland / Stream	w94 s96
n1	----	Tattnal	Glisson's Millpond	Echo 19	Metz Pond Pinelands	40	Osier	Sandhill Seep / Wooded Stream	w90 w93 w95
n2	----	Tattnal	Glisson's Millpond	Echo 19	North of Metz Pond Pinelands	42	Pelham	Pine Savanna / Stream	w90 w93 w95
n4	----	Liberty	Glennville NE	Echo 11	Between Bethel Cemetery & Bastogne Airstrip	27	Ellabelle	Wooded Stream	w90 w95
n5	----	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	33	Pelham	Pine / Cypress Savanna	w90 w95
n6	----	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	30	Pelham / Leefield	Cypress Dome / Savanna	w90 w95
n7	----	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	30	Ellabelle	Wooded Stream Head / Savanna	w90 w92 w95
n8	----	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	34	Pelham	Pine / Cypress Savanna	w90 w95
n9	----	Liberty	Glisson's Millpond	Echo 11	Sandhill Cemetery	27	Pelham / Leefield	Wooded Stream / Savanna	w90 w92 w95
n10	----	Tattnal	Glisson's Millpond	Echo 19	Bird's Creek	46	Osier	Wooded Stream / Savanna	w90 w93 w95
n11	----	Liberty	Glisson's Millpond	Echo 10	Sandhill Cemetery	34	Pelham	Cypress Dome / Savanna	w90 w95
n12	----	Liberty	Glisson's Millpond	Echo 10	Sandhill Cemetery	30	Pelham / Leefield	Pine Savanna	w94
n13	----	Tattnal	Glisson's Millpond	Echo 19	Northeast of Metz Pond Pinelands	42	Fuquay / Osier	Wooded Stream / Sandhill Seep	w93 w94
n14	----	Evans	Glisson's Millpond	Echo 17	Sandhill Cemetery	37	Leefield	Wooded Stream / Savanna	w92 s93 w94 s95

APPENDIX B: List of Plant Species Associated with *B. Atropurpurea* at Fort Stewart (Helton in Prep)

Herbaceous species

Agalinis sp. GERARDIA
Andropogon virginicus. BROOMSTRAW
Aristida spiciformis. THREE-AWNED GRASS
Aster paludosus. ASTER
Cacalia sp. INDIAN PLANTAIN
Carex sp. SEDGE
Coreopsis sp. TICKSEED
Erianthus gigantea. PLUME GRASS
Eriocaulon decangulare. HATPIN
Eupatorium sp. THOROUGHWORT
Euthamia minor. RAYLESS GOLDENROD
Helianthus sp. SUNFLOWER
Lachnanthes virginiana. REDROOT
Lobelia glandulosa. LOBELIA
Osmunda cinnamomea. CINNAMON FERN
Panicum sp. PANIC GRASS
Rubus betulofolius. BLACKBERRY
Sarracenia minor. HOODED PITCHER PLANT
Schizachyrium sp. BLUESTEM
Sporobolus sp. DROPSEED
Woodwardia aerolata. NETTED CHAIN FERN
Xyris spp. YELLOW-EYED GRASS

Shrub species

Acer rubrum . RED MAPLE
Baccharis halimifolia . GROUNDSEL TREE
Cliftonia monophylla . BLACK TITI
Hypericum sp. ST. JOHN'S WORT
Ilex glabra . GALLBERRY
Lyonia lucida . FETTERBUSH
Magnolia virginiana . SWEET BAY
Myrica cerifera . WAX MYRTLE
Myrica heterophylla . BAYBERRY
Persea borbonia . RED BAY

Pinckneya pubens. HAIRY FEVER TREE
Rhus copallina. WINGED SUMAC
Vaccinium corymbosum. HIGHBUSH BLUEBERRY

Tree species

Acer rubrum. RED MAPLE
Liriodendron tulipifera. TULIP TREE
Magnolia virginiana. SWEET BAY
Nyssa sylvatica. BLACK GUM
Persea borbonia. RED BAY
Pinus elliottii. SLASH PINE
Pinus palustris. LONGLEAF PINE
Pinus taeda. LOBLOLLY PINE
Quercus spp. OAK
Taxodium ascendens. POND CYPRESS

APPENDIX C: Soil Analysis for the *B. Atropurpurea* Populations at Fort Stewart

Soil sample analysis for *Balduina atropurpurea* populations at Fort Stewart, Georgia (Halward et al. in prep).

Popula	Laye	pH	Lime	% OM	NO_3-N	P	K	Zn	Fe	Mn	Cu	Texture
1	N/A	3.9	low	2.1	13	0.9	0.1	0.2	116.0	0.2	0.2	sl
2b	top	4.0	low	2.0	8	1.2	0.1	0.4	129.0	0.2	0.4	sl
2b	botto	4.5	low	1.0	5	0.6	0.1	0.1	32.2	0.1	0.5	sl
2c	top	4.2	low	3.6	14	1.2	2.1	0.7	121.0	0.3	0.7	sl
2c	botto	4.4	low	1.7	5	0.9	0.1	0.3	59.5	0.1	0.3	sl
3a	top	3.9	low	6.5	38	0.9	7.3	1.7	232.0	1.4	2.2	sl
3a	botto	4.1	low	2.3	6	0.6	0.1	0.3	93.8	0.2	0.9	sl
3c	top	4.7	low	2.8	12	1.8	19.1	0.7	207.0	1.2	2.0	sl
3c	botto	4.3	low	1.0	4	0.6	0.1	0.1	130.0	0.1	0.2	scl
3e	top	4.0	low	4.1	7	0.9	0.1	0.5	132.0	0.1	0.6	sl
3e	botto	4.3	low	2.1	4	0.6	0.1	0.2	49.7	0.1	0.3	sl
4	N/A	4.6	low	2.7	7	1.8	0.1	0.8	99.4	0.2	5.0	sl
5u	N/A	4.0	low	4.8	9	1.2	0.6	0.2	86.1	0.2	0.2	sl
5m	top	4.4	low	3.0	3	1.2	5.6	0.4	210.0	0.4	1.3	sl
5m	botto	4.6	low	1.3	2	0.2	0.1	0.2	69.7	0.2	1.3	sl
n1	top	4.6	low	3.2	19	1.2	10.4	0.4	127.0	0.7	1.0	sl
n1	botto	4.7	low	1.1	3	0.9	0.1	0.1	63.8	0.1	0.2	sl
n2	N/A	3.9	low	2.8	29	1.2	11.2	0.5	187.0	0.5	0.8	sl
n3	N/A	4.2	low	1.5	8	2.5	0.1	0.5	73.8	0.9	0.4	sl
n4	top	4.3	low	3.0	30	2.5	11.3	1.6	337.0	1.4	1.0	sl
n4	botto	3.9	low	4.9	41	1.5	0.3	0.8	290.0	0.8	1.8	sl
n5	top	4.4	low	2.8	11	1.2	0.1	0.3	135.0	0.3	0.2	sl
n5	botto	4.5	low	2.1	4	12.7	0.1	0.2	78.2	0.2	0.4	sl
n6	top	4.7	low	1.9	5	26.2	2.1	0.3	38.0	0.4	0.5	sl
n6	botto	5.0	low	1.3	1	9.9	0.1	0.1	14.4	0.1	0.2	sl
n7	N/A	4.1	low	2.5	26	1.5	0.1	0.5	95.4	0.7	0.2	sl
n8	N/A	4.1	low	4.8	29	1.2	0.1	1.3	163.0	1.0	0.5	sl
n9	N/A	4.3	low	3.1	13	1.2	0.1	0.4	115.0	0.3	0.3	sl
n10	top	4.3	low	6.3	36	1.2	11.1	1.2	349.0	1.5	0.9	sl
n10	botto	4.5	low	1.9	6	0.9	0.1	0.2	66.8	0.2	0.5	sl
n11	top	4.0	low	4.7	11	0.6	0.1	0.6	101.0	0.4	0.6	sl
n11	botto	4.3	low	3.8	3	2.5	0.1	0.5	64.0	0.3	0.5	sl
n12	top	4.5	low	6.7	2	2.1	12.5	0.4	126.0	0.3	0.5	sl
n12	botto	4.4	low	3.2	2	0.6	0.1	0.2	40.7	0.1	0.3	sl
n13	N/A	4.6	low	4.2	20	2.1	0.1	0.8	152.0	2.2	1.3	sl

*Layer = top 0-2.5 cm and bottom 2.6-5.0 cm of soil core; %OM = % organic matter; NO_3-N = nitrate nitrigen; P = phosphorous; K = potassium; Zn = zinc; Fe = iron; Mn = manganese; Cu = copper; Texture estimates are sl=sandly loam, and scl = sandy clay loam; % OM, NO_3-N, P, K, Zn, Fe based on NH_4HCO_3-DPTA extract mg/kg; population 5u = upper region of population 5 and population 5m = middle region of population 5.

APPENDIX D: Population Data, Vegetative Data, and Reproduction Results per Population and Overall in 1995

Population Data

	Population	N	Mean ± SE	Range
Number of Genets per Quadrat	1	50	3 ± 0.33	1 - 10
	2	90	2 ± 0.17	1 - 12
	3	90	3 ± 0.20	1 - 10
	4	30	5 ± 0.85	1 - 21
	5	30	5 ± 0.65	1 - 17
	Overall	290	3 ± 0.16	1 - 21
CI Calculated Genet Density	1	50	0.13 ± 0.00	----
	2	90	0.24 ± 0.00	----
	3	90	0.15 ± 0.00	----
	4	30	0.25 ± 0.01	----
	5	30	0.16 ± 0.01	----
	Overall	290	0.18 ± 0.00	----

Vegetative Data

	Population	N	Mean ± SE	Range
Number of Ramets per Genet	1	50	4 ± 0.48	1 - 14
	2	90	3 ± 0.21	1 - 10
	3	90	3 ± 0.22	1 - 14
	4	30	2 ± 0.28	1 - 7
	5	30	4 ± 0.56	1 - 17
	Overall	290	3 ± 0.15	1 - 17
Number of Stems per Genet	1	50	2 ± 0.24	1 - 8
	2	90	2 ± 0.10	1 - 5
	3	90	2 ± 0.14	1 - 9
	4	30	1 ± 0.08	1 - 3
	5	30	2 ± 0.17	1 - 4
	Overall	290	2 ± 0.07	1 - 9

Vegetative Data (Continued).

	Population	N	Mean ± SE	Range
Stem Height per Ramet (cm)	1	50	83.09 ± 1.74	52.10 - 108.00
	2	90	83.01 ± 1.55	49.20 - 117.50
	3	90	72.55 ± 1.18	40.40 - 100.30
	4	30	74.23 ± 2.90	41.30 - 103.20
	5	30	72.42 ± 2.09	47.50 - 98.20
	Overall	290	77.77 ± 0.82	40.40 - 117.50
Basal Leaf Length per Ramet (cm)	1	49	11.43 ± 0.46	4.00 - 19.80
	2	88	13.16 ± 0.38	6.20 - 24.50
	3	87	10.75 ± 0.40	2.50 - 23.00
	4	30	11.39 ± 0.84	5.90 - 24.10
	5	29	11.65 ± 0.82	5.10 - 25.60
	Overall	283	11.78 ± 0.23	2.50 - 25.60
Basal Leaf Width per Ramet (cm)	1	49	0.90 ± 0.07	0.43 - 3.85
	2	88	0.79 ± 0.02	0.35 - 1.25
	3	87	0.75 ± 0.02	0.30 - 1.10
	4	30	0.74 ± 0.03	0.45 - 1.28
	5	29	0.79 ± 0.04	0.48 - 1.15
	Overall	283	0.79 ± 0.02	0.30 - 3.85

Reproduction

	Population	N	Mean ± SE	Range
Number of Inflorescences per Genet	1	50	6 ± 0.65	1 - 20
	2	90	5 ± 0.31	1 - 16
	3	90	4 ± 0.30	1 - 14
	4	30	3 ± 0.27	1 - 7
	5	30	3 ± 0.47	1 - 12
	Overall	290	4 ± 0.19	1 - 20
Number of Inflorescences per Ramet	1	50	3 ± 0.29	1 - 11
	2	90	3 ± 0.20	1 - 10
	3	90	3 ± 0.16	1 - 9
	4	30	3 ± 0.23	1 - 7
	5	30	2 ± 0.18	1 - 4
	Overall	290	3 ± 0.10	1 - 11

Reproduction (Continued).

	Population	N	Mean ± SE	Range
Number of Ray Flowers per Inflorescence	1	37	16 ± 0.52	10 - 23
	2	80	15 ± 0.31	10 - 22
	3	87	14 ± 0.28	9 - 20
	4	23	15 ± 0.51	11 - 22
	5	27	14 ± 0.73	2 - 22
	Overall	254	15 ± 0.18	2 - 23
Capitulum Width (cm)	1	37	2.14 ± 0.05	1.10 - 2.60
	2	80	2.15 ± 0.03	1.20 - 2.80
	3	87	2.12 ± 0.02	1.30 - 2.80
	4	23	2.09 ± 0.07	1.40 - 2.70
	5	27	2.00 ± 0.06	1.50 - 2.60
	Overall	254	2.11 ± 0.28	1.10 - 2.80

Population	1	2	3	4	5	Overall
Percent of Genets Flowering	60	73	65	57	39	61
Percent of Ramets Flowering	56	65	64	64	48	60

APPENDIX E: Summary Environmental Data for the *B. Atropurpurea* Populations at Fort Stewart

The number of quadrats per population representing type of disturbance, relative disturbance degree and relative light level in 1996.
DT = Disturbance Type, h = Human, n = Natural; DD = Disturbance Degree and L = Light, 1 = Low, 2 = Moderate, 3 = High.

		1	2a	2e	2f	3a	3b	3c	3d	3f	4	5a	5b	5c	6	n1	n2	n4	n5	n6	n7	n8	n9	n10	n11	n12	n13	n14	overall
DT	h	18	16	25	8	40	24	19	24	15	44	4	19	15	7	4	43	9	3	26	0	8	11	34	22	15	15	19	487
	n	32	34	25	13	10	26	31	26	25	6	8	25	11	11	15	3	35	7	24	1	4	36	6	29	35	35	6	519
DD	1	36	37	40	19	10	21	37	35	33	8	11	37	19	15	19	5	43	10	29	1	9	34	17	35	40	38	8	646
	2	11	6	2	0	9	19	8	7	6	10	1	6	5	3	0	5	0	0	12	0	1	3	18	8	6	7	5	158
	3	3	7	8	2	31	10	5	8	1	32	0	1	2	0	0	36	1	0	9	0	2	10	5	8	4	5	12	202
DT + DD	h1	5	4	15	6	2	3	8	11	10	2	3	12	9	4	4	2	8	3	5	0	5	1	11	6	5	4	2	150
	h2	10	5	2	0	7	11	6	5	4	10	1	6	5	3	0	5	0	0	12	0	1	2	18	8	6	7	5	139
	h3	3	7	8	2	31	10	5	8	1	32	0	1	1	0	0	36	1	0	9	0	2	8	5	8	4	4	12	198
	n1	31	33	25	13	8	18	29	24	23	6	8	25	10	11	15	3	35	7	24	1	4	33	6	29	35	34	6	496
	n2	1	1	0	0	2	8	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	19
	n3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	0	0	0	1	0	4
L	1	1	1	3	4	0	1	4	6	0	1	0	11	2	8	3	4	9	1	6	0	0	16	3	8	1	7	0	100
	2	11	13	4	9	1	5	6	3	2	7	12	9	7	6	6	5	25	0	7	1	3	12	6	18	11	11	16	216
	3	38	36	43	8	49	44	40	41	38	42	0	24	17	4	10	37	10	9	37	0	9	19	31	25	38	32	9	690
DT + L	h1	0	1	1	0	0	0	0	0	0	0	0	1	1	3	0	1	2	0	0	0	0	2	0	2	0	0	0	14
	n1	1	0	2	4	0	1	4	6	0	1	0	10	1	5	3	3	7	1	6	0	0	14	3	6	1	7	0	86
	h2	5	2	1	4	0	2	2	1	0	3	4	2	1	1	0	5	6	0	1	0	1	2	4	5	0	0	12	60
	n2	6	11	3	5	1	3	4	2	2	4	8	7	6	5	6	0	19	0	6	1	2	10	2	13	11	11	4	152
	h3	13	13	23	4	40	22	17	23	15	41	0	16	13	3	4	37	1	3	25	0	7	7	30	15	15	15	7	409
	n3	25	23	20	4	9	22	23	18	23	1	0	8	4	1	6	0	9	6	12	0	2	12	1	10	23	17	2	281
DD + L	1/1	1	0	2	4	0	1	4	6	0	1	0	11	2	7	3	4	9	1	6	0	0	14	3	7	1	7	0	94
	2/1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	6
	3/1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	4
	1/2	7	12	3	7	1	4	4	3	2	5	11	9	6	6	6	0	24	0	6	1	2	9	4	15	11	11	6	175
	2/2	3	0	0	0	0	0	1	0	0	1	1	0	0	0	0	3	0	0	1	0	1	0	2	1	0	0	4	18
	3/2	1	1	1	2	0	1	1	0	0	1	0	0	1	0	0	2	1	0	0	0	0	3	0	2	0	0	6	23
	1/3	28	25	35	8	9	16	29	26	31	2	0	17	11	2	10	1	10	9	17	0	7	11	10	13	28	20	2	377
	2/3	8	6	2	0	9	19	7	7	6	9	0	6	5	2	0	2	0	0	11	0	0	2	16	7	6	7	1	138
	3/3	2	5	6	0	31	9	4	8	1	31	0	1	1	0	0	34	0	0	9	0	2	6	5	5	4	5	6	175
DT + DD + L	h/1/1	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	1	2	0	0	0	0	1	0	1	0	0	0	9
	h/2/1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	h/3/1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	4
	n/1/1	1	0	2	4	0	1	4	6	0	1	0	10	1	5	3	3	7	1	6	0	0	13	3	6	1	7	0	85
	n/2/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
	n/3/1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	h/1/2	1	1	0	2	0	1	0	1	0	1	3	2	0	1	0	0	5	0	0	0	0	0	2	2	0	0	2	24
	h/2/2	3	0	0	0	0	0	1	0	0	1	1	0	0	0	0	3	0	0	1	0	1	0	2	1	0	0	4	18
	h/3/2	1	1	1	2	0	1	1	0	0	1	0	0	1	0	0	2	1	0	0	0	0	2	0	2	0	0	6	22
	n/1/2	6	11	3	5	1	3	4	2	2	4	8	7	6	5	6	0	19	0	6	1	2	9	2	13	11	11	4	151
	n/2/2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	n/3/2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
	h/1/3	4	3	15	4	2	2	8	10	10	1	0	9	8	1	4	1	1	3	5	0	5	0	9	3	5	4	0	117
	h/2/3	7	5	2	0	7	11	5	5	4	9	0	6	5	2	0	2	0	0	11	0	0	2	16	7	6	7	1	120
	h/3/3	2	5	6	0	31	9	4	8	1	31	0	1	0	0	0	34	0	0	9	0	2	5	5	5	4	4	6	172
	h/1/3	24	22	20	4	7	14	21	16	21	1	0	8	3	1	6	0	9	6	12	0	2	11	1	10	23	16	2	260
	h/2/3	1	1	0	0	2	0	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18
	h/3/3	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	3

APPENDIX F: F Statistics from DDA Pairwise Comparisons

F statistics for all possible pairwise comparisons among populations in 1996 (Numerator DF=4, Denominator DF=973).

	1	2a	2	2f	3a	3b	3c	3d	3f	4	5a	5b	5c	6	n1	n2	n4	n5	n6	n8	n9	n10	n11	n12	n13	n14
1	0																									
2a	0.55	0																								
2e	3.10	1.70	0																							
2f	2.44	1.92	4.78	0																						
3a	4.22	3.58	3.34	3.85	0																					
3b	4.13	2.95	4.29	1.37	2.46	0																				
3c	3.66	1.65	1.12	4.32	5.77	6.06	0																			
3d	2.24	1.64	3.34	1.39	1.09	0.68	4.69	0																		
3f	4.04	3.22	5.48	0.88	2.35	0.33	6.74	0.59	0																	
4	5.99	5.14	2.68	5.92	1.43	3.23	6.67	2.96	4.2	0																
5a	2.92	2.10	1.14	2.65	0.64	0.99	2.22	1.10	1.42	0.35	0															
5b	1.49	3.28	8.54	2.71	7.87	6.97	8.76	4.64	5.68	11.1	5.41	0														
5c	3.44	2.97	4.96	0.76	2.74	0.36	6.16	0.94	0.17	3.78	1.65	4.38	0													
6	13.8	12.6	13.9	5.61	8.15	5.50	16.0	7.25	4.49	9.05	4.04	14.7	3.55	0												
n1	0.61	1.36	2.76	3.47	4.68	5.05	2.97	3.52	5.18	5.42	3.75	1.22	4.60	13.8	0											
n2	3.90	2.90	2.89	2.53	1.06	0.45	5.34	0.65	0.99	1.22	0.43	7.47	1.10	6.19	4.70	0										
n4	3.48	3.78	6.96	1.33	2.79	1.27	9.00	0.96	0.58	4.91	2.20	3.91	0.45	5.52	4.45	1.76	0									
n5	2.10	2.17	3.93	2.45	3.68	4.64	2.78	3.04	3.94	6.08	3.91	2.08	4.24	9.86	1.97	4.71	3.92	0								
n6	0.95	0.10	2.12	1.62	4.33	3.08	1.50	1.94	3.28	6.17	2.32	3.64	3.01	12.6	1.69	3.36	4.17	2.09	0							
n8	0.28	0.61	1.42	1.45	1.71	1.29	2.21	0.92	1.53	1.84	1.68	0.87	1.32	6.64	0.61	1.23	1.10	2.40	0.86	0						
n9	13.2	12.1	13.8	9.11	8.39	15.5	12.1	10.5	12.2	15.5	5.42	15.4	11.8	16.9	9.72	13.4	13.6	1.96	12.3	7.08	0					
n10	0.59	1.78	3.53	4.24	4.25	6.04	4.71	3.48	5.84	5.68	3.38	1.83	5.05	15.4	0.39	5.00	4.67	2.21	2.53	0.52	11.7	0				
n11	2.04	0.63	0.53	2.72	2.64	2.41	0.99	1.66	3.20	3.19	1.10	6.45	3.12	11.6	2.61	1.89	4.61	3.10	0.77	1.08	12.2	3.26	0			
n12	0.21	0.37	3.30	1.57	4.50	3.18	3.48	1.85	3.14	6.37	2.82	1.64	2.63	12.5	1.04	3.50	2.95	2.22	0.53	0.33	14.0	1.42	1.80	0		
n13	1.51	3.59	6.84	5.63	8.48	10.2	7.64	6.72	9.35	10.6	5.46	1.58	7.48	19.8	0.22	9.16	7.47	2.33	4.41	0.97	16.3	0.51	6.38	2.59	0	
n14	6.59	7.23	9.94	7.20	7.73	12.4	8.51	8.17	10.3	12.8	6.48	6.58	10.1	18.1	4.70	11.3	9.85	0.57	7.53	4.83	2.24	5.28	8.90	7.53	6.07	0

APPENDIX G: P Values from DDA Pairwise Comparisons

Significant adjusted P values (α=0.0325) from DDA all possible pairwise comparisons among populations in 1996 (***).

	1	2a	2	2f	3a	3b	3c	3d	3f	4	5a	5b	5c	6	n1	n2	n4	n5	n6	n8	n9	n10	n11	n12	n13	n14
1	0																									
2a		0																								
2e			0																							
2f				0																						
3a					0																					
3b						0																				
3c					***	***	0																			
3d								0																		
3f							***		0																	
4	***			***			***			0																
5a											0															
5b			***		***	***	***			***		0														
5c							***						0													
6	***	***	***		***		***	***		***		***		0												
n1														***	0											
n2												***		***		0										
n4			***				***										0									
n5										***				***				0								
n6										***				***					0							
n8														***						0						
n9	***	***	***	***	***	***	***	***	***	***		***	***	***	***	***	***		***	***	0					
n10						***			***					***							***	0				
n11												***		***							***		0			
n12										***				***							***			0		
n13			***		***	***	***	***	***	***			***	***		***	***				***		***		0	
n14	***	***	***	***	***	***	***	***	***	***	***	***	***	***		***	***		***				***	***	***	0

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