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RECOVERY OF THE THREATENED ECONOMIC PLANT GOLDENSEAL (*HYDRASTIS CANADENSIS*)

EVALUATION OF POPULATION TRENDS, LIMITING FACTORS, AND TRANSPLANTING WITH SIMULATED DISTURBANCE

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For my dad

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Abstract

The native woodland herb, goldenseal (*Hydrastis canadensis*), is threatened in Canada. Recovery to a non-risk category is particularly desirable given its medicinal and potential crop value. Woodland herbs probably evolved in an environment with severe and frequent disturbances, including massive floods and impacts of extinct and extirpated fauna. Lack of specific disturbance may limit growth and spread. Ecological observations and analysis (Part I) refined this hypothesis. Comparison of recent and 10 year old surveys, and stem numbers over two years, indicated lack of growth and spread. Pollination and dispersal appeared non-limiting based on observation of abundant polylectic bees and syrphid flies and rapid removal of fruit. Chi-square tests, comparing frequencies of goldenseal and random points along transects throughout woodlands, revealed a significant association with paths and edges. This suggested a positive disturbance effect and justified an extensive random block field experiment (Part II). Each block contained four one metre square treatment plots: substrate turned, fertilized, both, and control. Transplants in 100 blocks and seeds in 40 blocks were evaluated over two years. Multi-factor analysis of variance, through an extension of the Kruskal-Wallis test, followed by multiple comparisons using modified Tukey tests, was used to analyse the highly variable and discontinuous data. Significantly greater growth occurred in substrate turnover plots after one year. Each year soil turnover plots had significantly more fruit, and after two years, soil turnover + fertilization plots had significantly more fruit and seeds per fruit. Lack of significant increase in germination was attributed to dry conditions. Results represent the first experimental evidence for a positive effect of substrate disturbance on growth and reproduction of a woodland herb exclusive of canopy gap effects. Management

involving transplanting with substrate turnover may be essential for recovery according to projection matrix analysis (Part III) of two sets of transition years for 14 populations. The overall growth rate was 0.986 +/- 0.133 (SD) per year. Survival of established stems and vegetative propagation were critical for spread given lack of seedling development. The hypothesis that some woodland herbs are rare due to lack of certain disturbances that were more prevalent in the past was supported.

Résumé

Plante herbacée indigène des régions boisées, l'hydraste du Canada (*Hydrastis canadensis*), est une espèce menacée au Canada. Le récupération de celle-ci à une catégorie de non-risque est particulièrement souhaitable à cause de sa valeur médicinale et le potentiel que cette culture promet. Les plantes herbacées forestières ont probablement évolué dans un environnement ayant de sévères et fréquentes perturbations, comprenant aussi des inondations massives, ainsi que les impacts de la faune éteinte et extirpée. Le manque de perturbations spécifiques pourrait limiter leur croissance ainsi que leur propagation. Des observations et analyses écologiques (partie I) confirment cette hypothèse. Le manque de croissance et de propagation des populations a été démontré en comparant des relevés récents et de 10 ans passés, ainsi que par les tendances du nombre de tiges sur deux ans. La pollinisation et dispersion sont apparues non-limitantes basé sur l'observation d'abeilles polylectiques abondantes et de mouches syrphides et le prélèvement rapide des fruits par les animaux. Les tests du Chi-carré, comparant la fréquence des points de présence d'hydraste du Canada et des points aléatoires le long de transects à travers les boisés, ont indiqué une association significative avec les sentiers et les bordures. Cette évidence a suggéré que les perturbations a un effet positif et justifié une expérience sur terrain en blocs aléatoires (partie II). Des transplantations dans 100 blocs et des ensemencements dans 40 blocs ont été évalués sur une période de deux ans dans quatre parcelles de traitement, incluant un dont le substrat était retourné, un avec fertilisation, un avec sol retourné et fertilisé, et un un témoin. L'analyse de variance à facteurs multiples, par une extension de tests de Kruskal-Wallis, suivie de comparaisons multiples en utilisant des tests modifiés de Tukey, a été utilisée à cause de la grande variabilité des données et des données manquantes. Une croissance significativement plus grande s'est produite la première année dans le traitement dont le sol avait été retourné. À chaque année le traitement avec sol retourné a donné significativement plus de fruits. Le traitement sol retourné et fertilisé a donné significativement plus de fruits et plus de graines par fruit après deux ans. Le manque d'augmentation significative de la germination est attribué aux conditions sèches. Les résultats représentent la première évidence expérimentale que la perturbation du substrat a un effet positif sur la croissance et la reproduction d'une plante herbacée forestière, hormi les effets de troncés de la canopée. L'aménagement impliquant la transplantation avec substrat retourné peut être essentielle pour la récupération, selon l'analyse de matrice de projection (partie III) de deux séries de transitions pour 14 populations. La moyennne des taux de croissance a été un déclin de 0.986 +/- 0.133 (écart type). La survie des tiges établie et la propagation végétative étaient critiques puiqu'il y avait un manque de développement de semis. L'hypothèse voulant que certaines plantes herbacées forestières soient rare dû au manque de certaines perturbations, qui était plus abondantes par le passé, a été appuyée.

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1. Introduction

1.1 Background

Goldenseal (*Hydrastis canadensis* L.) is a perennial medicinal herb, native to North America. It occurs in rich, often moist deciduous woodland from southern Wisconsin to southern Vermont and south to Arkansas and northern Georgia (White & Dickson 1983, White 1991). It is a clonal plant that has a yellow, horizontal, irregularly knotty rhizome with numerous rootlets along its length. Stems arise from buds on the rhizome as well as root tips and reach up to 30 cm high. One to three palmate leaves, usually with five lobes and as wide as 30 cm, terminate the stem. The single white flower, a mass of stamens with no petals, opens in early May (in Ontario) and produces up to 30 small black seeds (2 - 4 mm) enclosed in a berry which ripens to red in July. Seeds remain dormant in the soil for approximately 10 months (from late July to early spring) at which time a cotelydon develops, and later, either in the first or second year, a single true leaf is produced (pers. obs.).

Primarily the rhizome, but also leaves and stems, are collected for medicinal use. Goldenseal has a long history of use as a herbal medicine based on ethnobotanical records of first nation peoples (Moerman 1986). This long history is also reflected by comprehensive records describing the history, chemistry, and effects of North American medicinal plants dating back to the early 1800s (e.g., Barton 1798 & 1804, Lloyd & Lloyd 1884-85, Millspaugh 1887). The roots were used by the Cherokee as a wash for local inflammations and as a decoction for general weaknesses, digestive disorders, and to improve appetite. The Iroquois used the roots to treat whooping cough, diarrhea, liver and heart trouble, fever, stomach pains, flatulence, and pneumonia (Moerman 1986, Foster 1991). Barton (1798 &1804) noted that goldenseal was a popular remedy in the United States and used as a bitter tonic and as a wash for eye inflammations. This was documented by Lloyd and Lloyd (1908) in their comprehensive review of the medicinal properties of goldenseal, the uses of which included the treatment of fevers, general weaknesses, gonorrhoea, inflammation and ulceration of the bladder, stomach and digestive disorders, inflammation of mucous membranes, and liver problems.

The major phytochemicals found in goldenseal include berberine, hydrastine, and canadine (Figure 1) as well as hydrastidine and canadaline (Lloyd & Lloyd 1908, Shideman 1950, Zwaving & de Jong-Havenga 1972, Messana *et al.* 1980, Hamon 1990, Abourashed & Khan 2000). Goldenseal extract and its isolated phytochemicals have been shown to demonstrate activity against six strains of bacteria (Scazzocchio *et al.* 2001), and berberine in particular, has demonstrated activity against a variety of bacteria (Amin *et al.* 1969, Akhter *et al.* 1977, Sack & Froehlich 1982, Zhu and Ahrens 1982, Rabbani *et al.* 1987, Sun *et al.* 1988a, 1988b), fungi (Mahajan, *et al.* 1982, Zhang & Shen 1989, Nakamoto *et al.* 1990, Arnason, pers. comm.) and protozoans (e.g., Subbaiah 1967, Gupte 1975, Ghosh *et al.* 1985, Kaneda *et al.* 1990, 1991). Anti-inflammatory activity, immune system stimulation, positive cardiovascular effects, and activity against chlamydia (*Chlamydia trachomatis*) have also been demonstrated by berberine (Sabir and Bhide 1971, Sabir *et al.* 1976, Babbar *et al.* 1982, Mohan *et al.* 1982, Kumazawa *et al.* 1984, Marin-Neto *et al.* 1988, Xu *et al.* 1989, Zhang & Shen 1989, Huang 1990a, 1990b, Riccioppo 1993, Ckless *et al.* 1995, Wu & Liu, 1995, Rehman *et al.* 1999, Abdel-Haq *et al.* 2000, Lau *et al.* 2001). These studies provide a rational basis for the antibacterial and anti-inflammatory uses of goldenseal as an antiseptic, hemostatic, diuretic, laxative, and anti-inflammatory for inflammations of the mucous membranes (Hamon 1990, Foster 1991, 2000) and support claims of benefits for the gastrointestinal tract, bronchial tubes, nasal passages, and bladder (Small & Catling 1999). In commercial formulations (pills, tinctures, teas, etc.), goldenseal is used for a variety of ailments including the common cold, nasal congestion, and infections, as well as to boost the immune system. Evidence suggests that goldenseal does not reduce the beneficial activity of other drugs highlighting another potential advantage of using goldenseal (Budzinski *et al.* 2000).

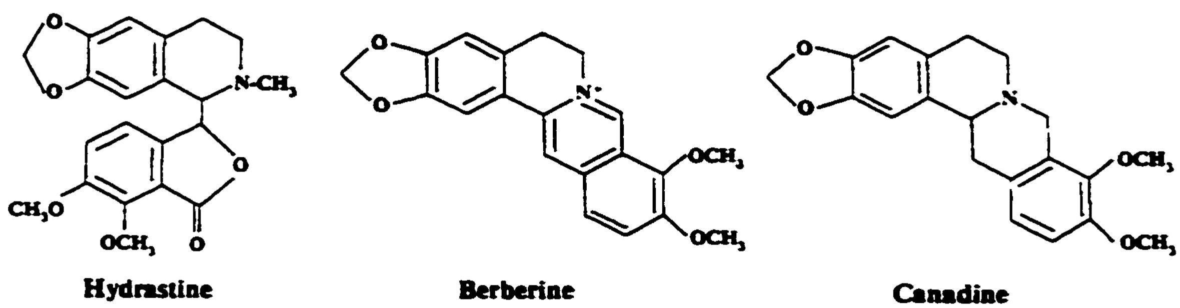

Figure 1. Structures of Major Phyotochemicals in Goldenseal (from Hamon 1990).

Goldenseal began to decline during the 1800s as a result of harvesting for medicinal use and declined further as a result of habitat loss (Small & Catling 1999). Renewed interest in herbal medicines has caused harvesting to increase since the early 1990s. The market demand for goldenseal has largely been met by harvest of wild populations in the United States (Foster 1991, USFWS 1997, Small & Catling 1999). Demand for goldenseal has been increasing dramatically (Foster 2000) and the plant continues to be one of the top six best-selling medicinal herbs (Robbins 1996, Small & Catling 1999, Foster 2000).

Goldenseal is perceived to be at a high risk of elimination due to excessive harvesting of wild populations to supply the market. It was listed as threatened in 1991, and re-evaluated as threatened in 2000, by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2001) due to a scattered distribution of a small number of populations, habitat loss, and the potential for unrestrained harvest of wild populations (White 1991). The U.S. Nature Conservancy has assigned a national rank of N4 and a global rank of G4, indicating that the plant is not susceptible to immediate threat; however, goldenseal is considered endangered, critically imperiled, imperiled, rare, or uncommon in all 27 states having native populations (USFWS 1997). Consequently, goldenseal was added to Appendix II of CITES (Convention on International Trade in Endangered Species) in 1997 (CITES 2000) which requires that goldenseal be artificially propagated for export (Canadian Wildlife Service 1999) and increased regulation of national and international trade.

The populations of goldenseal in Canada occur in southwestern Ontario at the northern limit of the species' range. These peripheral populations may be more fragmented and have lower and more variable densities compared to populations in the core of the range; however, the probability of extinction is not necessarily higher, and in fact may be lower, at the periphery compared to the core (Channell & Lomolino 2000). In general, remnant or fragmented habitats are valuable and worthy of protection for conserving plants (Järvinen 1982, Reznicek 1987). Thus, the Canadian populations are considered valuable for conservation of goldenseal in North America as a whole.

Due to its popularity and value as a medicinal plant, goldenseal has potential as a Canadian crop (Li & Oliver 1995, Small & Catling 1999, Sinclair & Catling 2001). Native populations are adapted to local climate and pests and may have other characteristics, including genetic variation, necessary to develop a viable Canadian crop. Crop development could reduce harvest of wild populations and prevent further decline.

1.2 Problem

It is desirable to recover goldenseal from the threatened category (to a category of lower concern) given its significance with respect to health, economy, and protection of biodiversity. Recovery involves increasing the size and/or number of populations (Hilton-Taylor 2000, Catling 2001a, Appendix A) which requires knowledge about the ecology of goldenseal. There is currently a serious lack of such knowledge according to the most recent review of the ecology and population biology of goldenseal (Gagnon 1999) and additional literature searches. Specifically, there are no population dynamics data available for goldenseal from anywhere within its range and only two papers on goldenseal ecology, one on the distribution, phenology, and biomass of goldenseal in an Indiana oak-hickory forest (Eichenberger & Parker 1976) and the other on the life history of goldenseal (Bowles 1891). Information on population dynamics, ecological factors that may limit population increase, and experimental tests of limiting factors are essential for recovery of goldenseal (USFWS 1997, White 1991, Gagnon 1999).

1.3 Goal, Objectives and Procedure

The **goal** of this thesis is to facilitate recovery of goldenseal from the threatened risk category to a category of lower concern by increasing its abundance. This requires data on status and limiting factors; thus, the main study **questions** are: (1) What is the population growth trend (decreasing, stable, or increasing)? and (2) What is limiting population increase?

The goal of the study will be met with the following **objectives**: (1) to investigate trends in population size and structure; (2) to identify ecological factors that may limit population increase and spread; (3) to develop and experimentally test an hypothesis related to limiting factors; and (4) to evaluate the need for implementation of recovery actions.

Preliminary observations indicate that disturbance is relevant to the recovery of goldenseal and therefore, the first step towards meeting the objectives is a review of disturbance ecology in order to provide a framework for a disturbance hypothesis. **Part I** of the study involves the collection and analysis of data on status and population trends, as well as ecological factors that may promote population increase, in order to refine the disturbance hypothesis. **Part II** involves a field experiment that tests the refined hypothesis. **Part III** investigates the dynamics of goldenseal populations using projection matrix models (Caswell 2001) to determine whether populations are increasing, decreasing, or simply persisting. This information contributes to the evaluation of the disturbance-simulation results of Part II and will suggest the importance of proceeding with recovery actions.

1.4 Review of Disturbance Ecology and Context of the Present Study

There is debate surrounding the definition of disturbance in ecology (e.g, White 1979, Picket & White 1985, Rykiel 1985, Jax 1999). For example, Grime (1977, 1979) provides a specific definition of disturbance as any event that removes biomass. Pickett and White (1985) define disturbance much more generally as any relatively discrete event in time that disrupts ecosystem, community, or population structure, and changes resources, substrate availability, or the physical environment. Rykiel (1985) seems to combine the two by defining disturbance as an event that can change community and ecosystem structure and composition by changing the physical environment and/or resource availability, which in the process usually removes or destroys biomass. Disturbance continues to be defined in this manner in current disturbance studies (e.g., Pyle 1995). Although the debate over the definition of disturbance may continue (e.g., Jax 1999), common effects of disturbance among systems have been revealed, namely increases in resources (e.g., light, nutrients, water, and substrate) and creation of patches (Pickett and White 1985).

1.4.1 History and Evolution of Disturbance Ecology

Although disturbance effects were observed in plant communities (e.g., Raup 1941, Jones 1945, Watt 1947), disturbance was not recognized as an important influence in vegetation dynamics until the late 1970s because the climax concept dominated the way in which vegetation was viewed (Clements 1916, 1920, 1928, Weaver & Clements 1929, Clements 1936). According to Clements, succession, the replacement of one kind of plant community by another, was the driving force in vegetation development and a result of competition between plants. Succession stopped when stability and equilibrium were reached. At this endpoint, the community was unchanging and in a state of balance, for example, between production and degradation, and dominated by species that established under their own canopies and replaced themselves. Species in the community were determined by climate, and in the absence of climatic change, the community persisted indefinitely. Thus, vegetation dynamics were a result of succession, which given enough time, produced a uniform, stable or unchanging, self-replicating community composed of the best competitors, that covered the entire landscape of any given region. Although Clements (1936) recognized that disturbance could slow or interrupt succession, he argued that it was not important because the destruction of vegetation was "selective, partial, or incomplete and continually renewed" and therefore, disturbance left "no permanent impress" or "modified the matrix (of plants) little or not at all". It is evident that disturbance had little consideration in vegetation dynamics under the climax concept.

The climax concept was altered in various ways over the years, for example from the monoclimax (a single climax determined solely by climate, Clements 1916), to polyclimax (mosaic of climaxes determined by soil moisture, nutrients, topography, slope exposure, and animal activity, Tansley 1935, Whittaker 1974, Smith 1990), and the climax pattern (mosaic of climaxes determined by the total environment of the ecosystem including species populations, biotic interactions, availability of colonizers, dispersal, soils, and climate, Whittaker 1953, Smith 1990). However, all of these variations of the climax concept implied an environment-vegetation equilibrium that remained stable within a region (White 1979). It was not until the late 1970s that an equilibrium view of vegetation development began to lose its dominance in plant ecology making way for consideration of disturbance as an important factor. An investigation of the development of the Hubbard Brook Experimental Forest after clear cutting indicated that catastrophic disturbance greatly modified plant communities and led to the introduction of the "shifting mosaic steady state" concept. Bormann and Likens (1979) proposed that, rather than reach equilibrium, mature forests attain a shifting mosaic steady state in which the amount of production, or biomass, fluctuates about a mean. In this view, mature forests are an array of irregular patches, composed of vegetation in different stages of development, as a result of disturbance, but the total production over all patches remains more or less the same over time. For a mature forest to reach a steady state however, patches must be relatively smaller than the homogeneous forest and disturbance must occur at regular intervals so that patches of various ages and sizes are distributed equally in time and space. Thus, the work of Bormann and Likens (1979) dispensed with an equilibrium concept of vegetation development but did not account for types of disturbances that are irregularly frequent or continuous and can create patches of all sizes within a forest, such as tree falls, impacts of fauna, and damage from lightning, snow, ice, wind, insect attacks or disease. These may also be important in vegetation dynamics.

As disturbance became increasingly recognized as ongoing and recurrent in certain ecosystems, it became difficult to accept equilibrium or steady state concepts as general models for predicting plant community composition and patterns. Watt (1947), Cooper (1913), and Jones (1945) are some examples of earlier ecologists who were less influenced by the equilibrium concept and observed disturbance effects in various communities. Connell (1978) argued, based on an investigation of tropical forests and coral reefs, that disturbances occur often enough that species assemblages seldom reach an ordered state and equilibrium may never be attained. Grime (1977, 1979) included disturbance as one of three important factors in his plant strategy theory which classified species according to their adaptations to disturbance, competition, and stress. Disturbance had implications for the kinds of strategies that would be adaptive and the overall predictability of vegetation patterns. White (1979) also noted, based on a review of natural disturbance processes in vegetation, that floras are rich in disturbance-adapted species and that disturbances have probably exerted selective pressures in the evolution of species strategies. He highlighted numerous important natural disturbances in North American vegetation, including fire, windstorms, ice storms, ice push on shores, cryogenic soil movement, alluvial processes, coastal processes, dune movement, saltwater inundation, landslides, lava flows, karst processes, as well as biotic disturbances such as insect outbreaks, digging, grazing, and beaver flooding. Other reviews (e.g., Knapp 1974, Grubb 1977, Miles 1979, Pickett 1980) provided a long catalogue of ecosystems in which natural disturbances play a fundamental role in plant community composition and development.

A new concept, which brought disturbance to the forefront as a significant factor involved in vegetation dynamics, soon emerged. Pickett and Thompson (1978) proposed the concept of "patch dynamics" which is similar to the shifting mosaic steady state concept but does not imply succession towards a steady state. In this view, forests are considered a series, or pattern, of patches, varying in size, internal homogeneity, and degree of similarity, that continuously change in time and space as a result of disturbance. The patch dynamics concept was adopted by Pickett and White (1985) in their comprehensive compilation and synthesis of information on natural disturbances in various ecosystems which contributed greatly towards the evolution of disturbance ecology. Various chapters show that natural disturbance affects both animals and plants in many different ecosystems, including coniferous forests (boreal, montane, and coastal plain), deciduous forests (all North American associations), evergreen forests (temperate and tropical), grasslands, shrublands, tundra, deserts, as well as marine, intertidal and subtidal communities. Other chapters demonstrate that disturbance affects individual organisms (growth, architecture, reproduction, and dispersal), populations (age, size, and genetic structure), communities (richness and dominance), and ecosystems (functions such as nutrient cycling and energetics). Pickett and White (1985) established disturbance as a major force in ecosystem dynamics by showing that it is common to many systems, operates at various spatial and temporal scales, and is continuous over many levels of biological organization, from individual organisms to entire ecosystems. The concept of patch dynamics which accounted for disturbance offered a new model for predicting plant community composition and structure.

A theoretical framework in which to view disturbance has been built upon the concepts of patch dynamics and disturbance regime (Pickett & White 1985). Patch dynamics emphasizes the changes within patches over space and time, the relationship of patches to one another and the surrounding matrix, and in the flows of organisms, materials, and energy among patches. Disturbance regime refers to the temporal and spatial pattern of creation of open or altered patches. The proposed framework consists of three parts: (1) measurable disturbance variables (duration, frequency, intensity and area); (2) response parameters (e.g., species richness, distribution of dominance, resources); and (3) context and constraints of disturbance in terms of system structure, resource base, life history characteristics, nature of competitive hierarchy, and landscape composition and configuration. Placing studies of the effects of disturbance within this framework will assist in the development of a disturbance theory that can predict effects.

Summary

- Disturbance was not recognized as an important influence on vegetation dynamics until the climax or an equilibrium view of vegetation development lost its grip on ecological thought.
- Large-scale or catastrophic disturbance became recognized as a major influence in the deciduous forest ecosystem through examination of clearcutting effects in the Hubbard Brook Experimental Forest. This slightly altered the concept of vegetation development by replacing the equilibrium endpoint with that of a steady state.
- Disturbance was observed to be regular, frequent, and continuous within many systems and equilibrium or steady state concepts became unacceptable means of explaining vegetation patterns.
- Ecologists began to realize that many species likely evolved adaptations to disturbance, given its prevalence in numerous ecosystems, and thus, in order to understand and

predict vegetation patterns, disturbance must be considered.

- The patch dynamics concept, which emphasized disturbance as a significant ecological factor, was soon introduced and offered a new model to predict vegetation patterns.
- The patch dynamics concept of an ecosystem as a matrix of patches that change over time and space due to disturbance, along with the concept of a disturbance regime or pattern of patch creation over time and space, comprised the proposed theoretical framework in which to view disturbance.
- The framework consisted of three components: measurable disturbance variables (area, frequency, duration, intensity), response parameters, and context and constraints of disturbance in the system.
- Investigation of disturbance, within the theoretical framework, especially in understudied systems, will contribute greatly towards a disturbance theory that enables or facilitates predictions of change.

1.4.2 Disturbance and Woodland Herbs

Numerous studies have demonstrated the importance of disturbance in forest herb communities; however, they have focussed primarily on the influence of canopy gaps with respect to light (e.g., Gysel 1951, Collins & Pickett 1982; Metzger & Schultz 1981; Davison & Forman 1982; Collins *et al.* 1985; Moore & Vankat 1986; Collins & Pickett 1988a, b; Brewer 1980; Reader & Bricker 1992; Hughes & Fahey 1991; Jenkins & Parker 1999). Increase in herb cover (Metzger & Schultz 1981; Davison & Forman 1982; Moore & Vankat 1986; Jenkins & Parker 1999), and increase (Gysel 1951), decrease (Davison & Forman 1982), or little change in herb diversity (Moore & Vankat 1986; Brewer 1980) and growth (Collins & Pickett 1988a) have been reported. Thus, the importance and often beneficial effect of canopy gaps is fairly well examined.

The need for information on effects of substrate disturbance on woodland herbs has been recognized by several authors. For example, Collins & Pickett (1988a) indicated the need for experimental studies involving soil disturbance in woodlands, and Hughes & Fahey (1991) emphasized the need for consideration of disturbance that affects the forest floor. The general lack of information about the ecology of forest herbs and their response to disturbance has been emphasized by both Metzger & Schultz (1981) and Collins *et al.* (1985).

Although the need for more information has been recognized by some ecologists, progress has been slow possibly because: (1) the fact that canopy removal is readily observed in woodlands, resulting in striking changes in the abundance of herbs often without soil disturbance (e.g., 64 - 100% of natural treefall openings are free of soil disturbance, Hughes & Fahey 1991), and (2) the relatively large amount of work on gaps, have both contributed to the impression that canopy disturbances are the only important disturbance processes affecting woodland herbs.

In addition to canopy disturbance, substrate disturbance is a potentially important influence that may also be beneficial to herbaceous woodland plants. Woodland herbs evolved in an environment with large, severe and frequent disturbances that altered the forest floor, including massive flooding of bottomland forests, fires, and impacts of extinct and extirpated fauna. It has been suggested that any eastern North American woodland herb is a candidate for consideration of beneficial effects of a variety of extinct and extirpated animals (Catling 2001b). These include passenger pigeons (*Ectopistes migratorius* L.), black bears (*Ursus americanus* Pallus), and very large and numerous pleistocene mammals (Kurtén & Anderson 1980) which may have caused soil disturbance, provided nutrients, and promoted colonization and spread, with or without alteration to the forest canopy.

1.4.3 Effects of Substrate Disturbance

Few studies have tested the effects of substrate disturbance on woodland herbs. Thompson (1980) found that they readily colonize (through seedling establishment or vegetative growth) pits, mounds, and decaying logs produced by treefalls. Cook & Lyons (1983) found that substrate disturbance stimulated germination, growth, and reproduction of northern downy violet (*Viola fimbriatula* Sm.) in two treefalls. They suggested that the present distribution of *V. fimbriatula* in habitats created by anthropogenic disturbances (woodland roads, hillsides, fields, gravel clearings, pastures) represented an opportunistic expansion from more natural disturbances such as treefalls, fire, and areas of soil erosion, in its primeval forest habitat. Although these studies were not experimental, in the sense of deciphering factors, and the effects were likely a combination of light, substrate disturbance, and/or other factors, they provide evidence for a beneficial role of substrate disturbance, in terms of population expansion and maintenance of certain woodland herbs.

The only experimental study to evaluate the effects of substrate disturbance on a woodland herb is that of Hughes (1992). He demonstrated that after removal of all co-occurring vegetation, colonization of yellow dog's-tooth violet (*Erythronium americanum* Ker Gawl ssp. *americanum*) increased through newly dispersed seeds, buried seeds, and vegetative growth. The increase occurred over three years on scarified and severely disturbed soils with a coinciding decrease on undisturbed soils. Hughes (1992) suggested that the effect of increased colonization was a combined result of canopy openness and soil disturbance. Collins & Pickett (1988b) also noted that soil disturbance may have influenced response of understory herbs to their experimental canopy gaps. The fact that certain species occurred only in gaps with soil disturbance suggested examination of either experimental or natural soil disturbance within gaps. Knowledge of the response of woodland herbs to substrate disturbance, especially exclusive of light effects, is limited.

The lack of experimental attention to substrate disturbance in woodlands contrasts with extensive research indicating beneficial effects in other systems, including grassland (Dolman & Sutherland 1994; Kotanen 1997), shortgrass steppe (Aguilera & Lauenroth 1995), sand dunes (Klinkhamer & de Jong 1988), old fields (Carson & Pickett 1990), oak savanna (Davis *et al.* 1995), subalpine meadows (Tardiff & Stanford 1998), and tall-grass prairie (Platt 1975; Rabinowitz & Rapp 1985, Rapp & Rabinowitz 1985). Similar to reported effects in woodlands, substrate disturbance promoted germination and early survival of certain plant species. Experimental investigation of the effects of substrate disturbance in woodlands may improve understanding of disturbance effects in relation to woodland herb ecology.

1.4.4 Impact of the Present Study with a Novel Hypothesis

The **hypothesis** that goldenseal will benefit from simulation of natural disturbance to the forest floor deserves testing based on the positive effect of substrate disturbance on *E. americanum*, *V. fimbriatula*, and other woodland herbs, and the suggestion that any woodland herb in eastern North America may benefit from disturbances that occurred naturally in the past. This study is the first to employ a field experiment to test a substrate disturbance hypothesis in relation to increased growth and reproduction of a woodland herb. It is also the first of its kind geared towards recovery and management of a rare woodland herb. The review of disturbance ecology indicates that the effect of substrate disturbance on woodland herbs is understudied and poorly understood. Results will increase knowledge of woodland herb ecology, especially rarity, in relation to disturbance effects, and contribute to disturbance theory by addressing the information gap concerning disturbances that affect the forest floor.

The present study is also significant to the use of disturbance and transplanting as a management tool for conservation of woodland flora. Consideration of disturbance as a beneficial and an important factor in the abundance and distribution of woodland herbs dramatically alters the view on how to best protect and manage biodiversity of woodlands in this region (i.e., northeastern United States and adjacent Canada). Simulation of natural disturbance as a management tool for protection of biodiversity, for example the use of fire, has been used less in this region compared to other areas in North America (Arno 1996, Catling & Sinclair 2000). In general, management of woodlands for biodiversity in this region assumes that undisturbed conditions, conceptually associated with mature woodlands, are optimal. This assumption is reflected in indices of floristic quality, in which plants are given "conservatism scores" or scores in relation to conservation importance. For example, species that are found in a wide variety of sites, including disturbed sites, are given a score from 0 to 3; species typically associated with a specific type of plant community but tolerant of moderate disturbance are given a score from 4 to 6; species that are usually associated with a narrow range of community types or sites that have undergone only minor disturbance are given a score from 7 to 8; and species with a high degree of fidelity to a narrow range of ecological parameters are given a score from 9 to 10. Thus, goldenseal and many other rare woodland plants have been given high conservatism scores, suggesting high conservation importance, based on the assumption that these species have a high degree of fidelity to undisturbed sites (e.g., Swink & Wilhelm 1979, Wilhelm & Ladd 1988, Oldham *et al.* 1995, Wilhelm & Masters 1995, Francis *et al.* 2000).

The results are relevant with respect to transplanting as a conservation tool as there are currently no reported transplanting projects involving rare or endangered woodland herbs (although Provencher, Nault and Gagnon transplanted green dragon (*Arisaema dracontium* (L.) Schott), a rare species of special concern (COSEWIC 2001), and results are in press in Biological Conservation) and effectiveness of transplanting ranges widely, from completely ineffective, when seeds do not germinate (Primack 1996) or whole plants or rhizomes die (Hall 1987; Fahselt 1988) to very successful, when transplants recruit new individuals and become self-maintaining populations (Pavlik *et al.* 1993; Falk *et al.* 1996). This study is the first to evaluate the effectiveness of transplanting with respect to conservation and management of a rare woodland herb.

The overall impact of the present study is the improvement of knowledge on the ecology of goldenseal which will aid in recovery and the development of effective conservation strategies, monitoring and management. In particular, the study will determine the current status of goldenseal populations in Canada, provide the only available data on pollination and dispersal mechanisms, assist in the identification of recovery actions through an evaluation and experimental test of potential limiting factors, and evaluate the need for recovery actions based on the first population dynamics data derived from projection matrix analysis. There will no longer be a serious lack of scientific data on the ecology of goldenseal. Further, experimental evaluation of substrate disturbance as a factor in goldenseal population dynamics will contribute to the protection of a threatened plant with potential health and economic benefits to Canada, possibly lead to improved woodland management to promote rare species, and contribute to disturbance theory.

Part I: Refinement of Hypothesis with Ecological Observations and Analysis

2. Materials and Methods

2.1 Population Trends

2.1.1 Population Survey

A database of location information was compiled from herbarium collections across Ontario (CAN, DAO, TRT, HAM, WAT, UWO, QK, acronyms from Holmgren *et al.* 1990) as well as from discussion with environmental planners and local biologists. Sites were visited from May 8 to June 6, 1998, when plants had mostly completed flowering and the distinctive leaves had expanded. To locate plants, search paths, approximately 10 m wide, were used, either in parallel or in series of concentric circles around a patch. Patches were marked with flagging tape and latitude and longitude were recorded using a hand held Trimble Scout GPS and 1:50 000 topographic maps. Populations were defined as occurrences at least 0.5 km apart (i.e., in separate woodlots) which corresponds to the definition of a population as a group of interbreeding individuals that occupy a given area at the same time (Curtis & Barnes 1989) and assumes that berries are dispersed within the same woodlot and pollinators (small bees and flies, see Section 3.2.2) do not travel more than 0.5 km. Population size (number of patches and stems) was estimated by direct count (Sutherland 1996), and the number of flowering and non-flowering stems were recorded. The number of stems (ramets) rather than plants (genets) were counted due to disturbance required to identify rhizome connections and the possibility that entire patches consisted of a single plant. In small patches of goldenseal, all stems were counted directly and the error on population size was estimated as two stems overlooked for every 20 stems. In large patches of goldenseal (> 10 m^2), population size was estimated by multiplying the average number of stems in randomly placed 1 m^2 quadrats by total estimated patch area. The total patch area was estimated by pacing the length and width of a patch (1 pace ≈ 1 m) and using an appropriate area formula based on the shape of the patch. The error in population size associated with this method was estimated as +/- 5% and applies only to two populations (Sites 3 and 6, Table 4, Section 3.3.3). The number of populations and population sizes were compared to previous survey results.

Using newly acquired information on habitat derived from the survey of re-located sites, including tree species, herbaceous plant associates, topography, and shade as well as proximity to a water body or drainage area, 11 sites were selected (on the Maitland, Thames, and Bayfield Rivers near Parkhill, Komoka, Grimsby, and Dunnville) and searched for goldenseal to determine the extent to which populations might have been overlooked and the extent to which new populations are establishing.

2.1.2 Stem Counts

In order to examine trends in population size and structure, a 1m^2 quadrat was placed towards the edge (i.e., not in the dense centre or sparse edge) of a single patch within each of 14 populations in May of 1998. Site numbers that coordinate with a file maintained by the Chairman of the Subcommittee for Plants of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) are provided rather than exact locations for conservation reasons. Each quadrat was permanently marked with four aluminum pins and a numbered aluminum tag. All stems were mapped within each quadrat according to the following size classes which were selected based on reproductive state: small (immature stem with single leaf ≤ 12.5 cm in width); large (mature stem with single leaf > 12.5 cm in width); and flowering (mature flowering stem with two or more leaves). The flowering stems are produced by larger rhizomes which are presumed to be the oldest. The smallest stems are generally associated with small rhizomes or root tips. Presence or absence of seedlings was noted. Due to the clonal nature of the plant, all of the stems in the quadrat may have developed from a single individual but determination of individuals or genotypes was beyond the scope of the study. In May of 2000, the 14 quadrats were revisited and remapped according to the same size classes. In July of both years, quadrats were revisited to record fruiting stems. The quadrat maps developed in 2000 were compared to those developed in 1998 to document any change in stem numbers and size classes.

2.2 Reproductive Ecology - Pollination and Dispersal

2.2.1 Pollination System Experiments

In 1999, prior to blooming, 11 plants with flower buds were collected at random from sites near Bothwell (42° 38' N, 81° 52' W in Zone Tp. of Kent Co.) and Durham (45° 10' N, 80° 49' W in West Grey Tp. of Grey Co.), and manipulated as described below to determine the relative importance of self-pollination. Only 11 plants were used due to the threatened status of the plant and use of a larger sample was inappropriate for these preliminary experiments.

Four plants were isolated in a glasshouse and their anthers were removed. Three plants were placed separately outside in a natural setting where no goldenseal occurs so that only self-pollination via agitation or insects was possible. Within flowers of four plants, pollen was transferred intraflorally, using a paint brush. These flowers were isolated from pollinators using nylon netting and tubes.

2.2.2 Pollination and Dispersal

During the first week of May, 1999, observations were made at four sites named according to the nearest town or village (latitude and longitude given): Amherstburg (42° 06' N, 83° 06' W in Malden Tp. of Essex Co.), Arner (42° 02' N, 82° 49' W in Gosfield South Tp. in Essex Co.), Watford (42° 57' N, 81° 53' W in Warwick Tp. of Lambton Co.), and Uttoxeter (43° 02' N, 82° 03' W in Plympton Tp. of Lambton Co.). Again, latitude and longitude of the exact sites are not provided for conservation reasons.

Insect activity was noted in the field during morning and afternoon periods on May 5th and 6th. Lengths of observation periods ranged from 20 minutes to 2.5 hours, depending on amount of insect activity and the density of plants in bloom. Some of the observation periods were short but were the only periods appropriate for activity over a period of many hours. Insect pollinators may provide pollination service very rapidly over rather unpredictable interludes of suitable conditions as noted by Schemske *et al.* (1978); therefore, observations need not necessarily be made over long periods of time.

At each site, during the specified time period below, all visitors and pollinators seen were recorded. An insect that visited only one flower was defined as a visitor, whereas, an insect that visited two or more flowers consecutively (permitting pollen transfer) was defined as a pollinator. Three or less of each pollinator class were collected to enable accurate identification and to minimally influence the pollination of the threatened plant. Insects were labelled, identified, and placed in the Canadian National Collection, maintained by Agriculture Canada in Ottawa.

At Amhertsburg, two patches with 121 and 500 flowers in late peak were observed for approximately two hours and 30 minutes during a sunny period, at about 20 °C, around 11 am, on May 5th. At Arner, one patch with 320 flowers in peak was observed for about two hours, during a sunny break just after a light shower, around 5 pm on May 5th. At Watford, one patch with 38 flowers just past peak, was observed for approximately 20 minutes, during a sunny period, at about 22 °C, around 12:30 pm on May 6th. At Uttoxeter, one patch with 48 flowers in peak was observed for approximately 20 minutes during a cloudy and windy period with short sunny breaks, at about 20 °C, around 2 pm on May 6th.

From July 10 to 24, when the fruit had ripened to red, patches were observed, at a distance of 10 to 15 m, for animal activity.

2.3 Ecological Aspects

2.3.1 Herb, Canopy, and Soil Layer

The quadrat sampling method was also used to collect data on ecological characteristics. In May, 1998, a 1 m^2 quadrat was placed towards the edge of a single patch (i.e., not in the dense centre nor on the sparse edge) within each of the 20 goldenseal populations in southwestern Ontario (14 of these were used for the stem counts in Section 2.1.2). The number of seedlings (if present), small (single leaf ≤ 12.5 cm in width); large (single leaf > 12.5 cm in width); and flowering (two or more leaves) stems were recorded within each quadrat. All plant species and percentage cover within the herb layer (< 1 m above ground) were recorded for each quadrat. Percentage cover was estimated as the proportion of the quadrat occupied by the aerial parts of plant species when viewed from directly above (Sutherland 1996). All tree species and their cover were recorded within a circle of 10 m radius around each patch in order to determine the dominant canopy species. Cover was estimated as the percentage area occupied by the canopy of each species projected onto the circle. Stems were examined for evidence of grazing by mammals which included torn or removed leaves and/or severed stems. With permission from landowners, a soil sample was collected from 13 of the quadrats, by pushing a metal cylinder to 9.5 cm depth into the soil. Soil samples were transported in bags to ACUTEST laboratories, in Ottawa, for standard soil analysis (OMAFRA 1988). Each sample was analysed for soil pH, organic matter (percent dry weight lost on ignition), available P (extracted with sodium bicarbonate), K, Mg, Ca (extracted with ammonium acetate), Mn (extracted with phosphoric acid), and Zn (extracted with DPTA, diethylenetriamine penta acidic acid). A laboratory that uses the soil analysis testing methods approved for use in Ontario by the Ministry of Agriculture, Food, and Rural Affairs (OMAFRA 1988) must be selected in order to replicate the soil analysis.

Multiple linear regression was used to examine the relationships between the environmental variables and the number of stems, in each size class and overall. The environmental variables included soil characteristics and the number and cover of plant associates. Calcium was raised to the second order in the multiple regression since plots of the relationships between calcium and the number of stems, in each size class and overall, revealed a curvilinear shape. Population sizes, in terms of number of stems and patches, were compared based on their dominant canopy species and soil type.

2.3.2 Habitat Size

Habitats and natural areas were delineated and scanned on aerial photographs using information from the photos and field reconnaissance. "Habitats" are defined as more or less continuous wooded situations within which site conditions did not appear to be restrictive to development of goldenseal. This concept of continuity admitted small gravel roads but not major roads or highways, nor major rivers over 10 m wide. For example, an abrupt change in habitat such as a steep slope with dry oak forest was considered a limit to habitat. The remarkable variability of goldenseal habitats was taken into account. "Natural areas" are broadly defined as more or less wooded areas, including those with major changes in plant associations, and were bounded by roads, open fields, agricultural land, and/or extensive water bodies. Relatively larger natural areas may provide more interaction opportunities relating to pollination and dispersal.

Linear regression was used to determine the relationship of habitat and natural area sizes to population size with respect to both number of stems and number of patches (one or more plants at least 5 m apart) at a location. Stems and patches within sites that shared the same natural area were pooled to evaluate the effect of natural area size. Number of stems was log-transformed in order to meet the assumptions of analysis of variance.

2.3.3 Spatial Analysis of Goldenseal Occurrence

During the 1998 field survey of populations, goldenseal was found in disturbed portions of each site, either next to recreational paths and drainage ways, within woodlot edges and previously flooded zones, in thickets and successional forests where logging had occurred, and on riverbanks, constructed dykes, and logging roads. In order to quantify and evaluate this circumstantial evidence of a positive disturbance effect, for patches of goldenseal (one or more plants at least 5 m apart), it was noted whether the approximate central point of the patch was within 5 m of a path (i.e., a track more than 1 m wide with compacted bare soil) or 10 m of a woodland edge beyond which an extensive open (non-treed) area existed. The 10 m limit is well within the < 20 m for floristic features related to edges reported by Burke and Nol (1998). Search method is not considered a factor which biases likelihood of goldenseal occurrence near paths and edges. Habitats in this study as well as hundreds of potential habitats in southwestern Ontario have been surveyed systematically by the authors and many other field botanists and these surveys have not been concentrated on paths and edges. Paths, which were associated with old tote roads, or tracks created by tractors or all-terrain vehicles, were considered to be randomly distributed throughout woodlands where goldenseal occurred. The entire habitat surrounding goldenseal patches was either flat, or uniformly and gradually hummocky, and characteristics of path locations appeared similar to the remaining habitat. Thus, the occurrence of goldenseal near paths is not considered a consequence of the path occurring in a different type of habitat.

Transects, with points every 20 m, were randomly set out in the habitat surrounding goldenseal patches to obtain a random sample of neighbourhood points with frequency data on proximity to paths and edges. Whether or not a transect point was within 5 m of a path or 10 m of an edge was noted. Frequencies of occurrences near paths and edges for the 638 neighbourhood points were compared with observed frequencies for 75 goldenseal points. Expected frequencies of goldenseal points near paths and edges for each population were calculated for each site based on the percentage of neighbourhood points near paths and edges. A Chi-square test then provided a significance value for frequency of goldenseal points near paths and edges at each site.

3. Results and Discussion

3.1 Population Trends

3.1.1 Population Survey

There are 26 known sites or populations of goldenseal (defined as 0.5 km apart) in Canada. They occur in nine major areas (Figure 2), mostly in the Carolinian Zone (Allen *et al.* 1990) which corresponds to Lake Erie Lowland Ecoregion 135. The three northernmost populations occur in the southwestern portion of adjacent Manitoulin-Lake Simcoe Ecoregion 134 of the Mixedwoods Plains Ecozone (Ecological Stratification Working Group 1995, Catling & Cayouette 1996).

The 1998 field survey of the 26 populations verified 21 extant populations. As indicated on the map (Figure 2), the distribution of goldenseal includes: three areas (near Crediton in 1942, near Wingham in 1889, and near Varna in 1975) where it could not found in 1998 (triangles); two areas which could not be surveyed in 1998 (half dots); and 21 areas where populations were found in 1998 (full circles). A site near Durham in Grey County is a substantial disjunction and believed to be a result of introduction. Failure to find new populations in 1998 (using the newly acquired ecological data from re-located goldenseal sites) suggests that few populations have been overlooked.

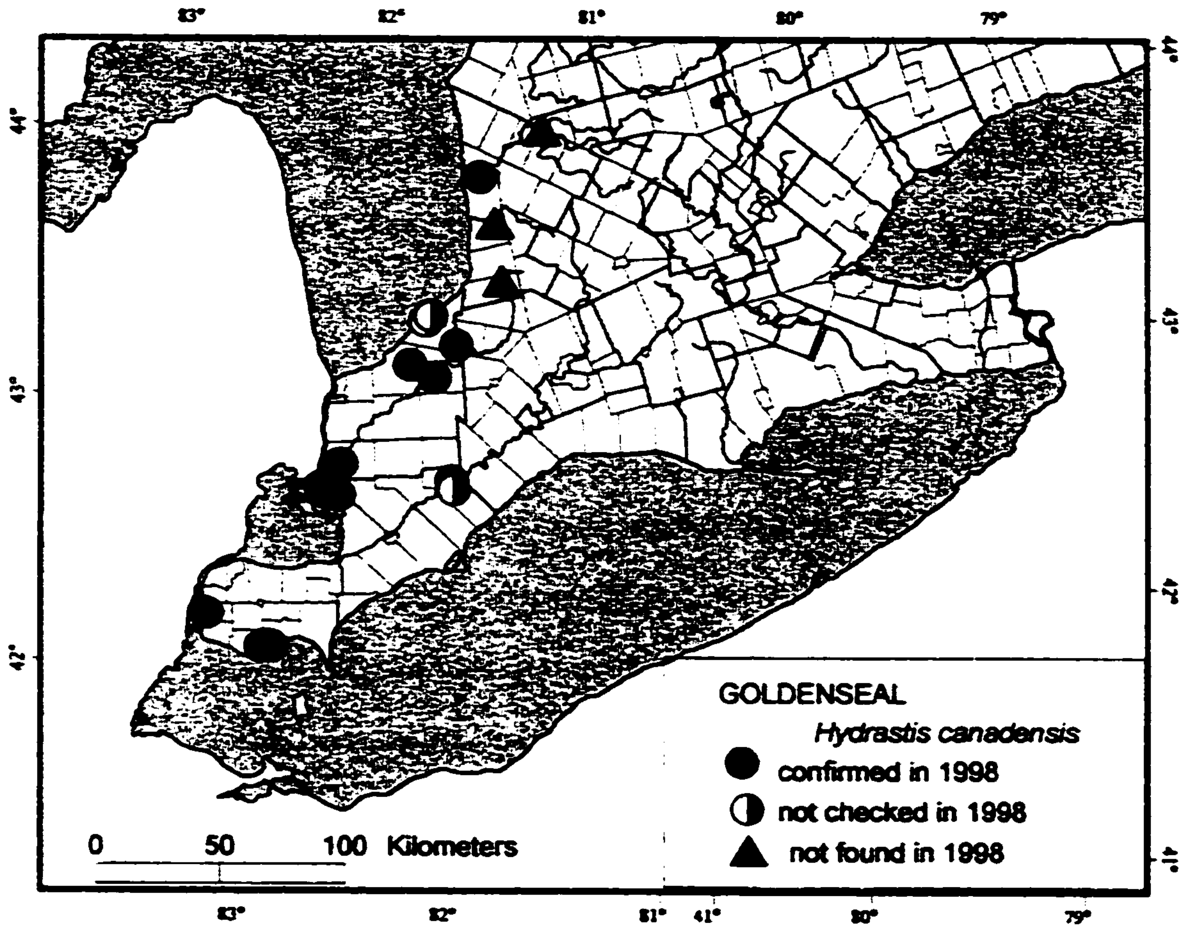

Figure 2. Distribution of goldenseal (*Hydrastis canadensis* L.) in southwestern Ontario based on specimens at CAN, DAO, TRT, HAM, WAT, UWO, and QK (acronyms from Holmgren *et al.* 1990). Triangles indicate areas (near Crediton in 1942, near Wingham in 1889, and near Varna in 1975) where goldenseal was not found in 1998; half dots indicate areas which could not be surveyed in 1998; and solid dots indicate areas where populations were found in 1998.

Although original survey data were not collected in such a way as to provide a basis for future comparisons, the 1998 survey suggests that there has been little if any decline in Canadian populations. The fact that only three of the 26 populations could not be re-located does not necessarily suggest extirpation given the relatively poor quality of the data available to re-locate populations (e.g., general location data referring to a goldenseal site near a town).

Furthermore, at least the same number of patches were found within each population since the last survey in 1991 (White 1991). An increase in population size is not proven, but nor is there any fully reliable evidence for decline. Stability or possible increase in patch size seems most likely.

Populations of goldenseal appear to be healthy; however, they do not appear to be spreading by seed at many sites. In these sites, goldenseal occurs only in isolated patches and evidence of seedling development was not found. Populations do not stretch out over large areas and the plant does not saturate the available habitat like so many other woodland herbs such as white trillium (*Trillium grandiflorum* (Michx.) Salisb.), cut-leaved crossbill (*Geranium maculatum* L.), yellow dog's-tooth violet (*Erythronium americanum* Ker Gawl. ssp. *americanum*), and wild leek (*Allium tricoccum* Aiton), even though its dominance (cover and stem number) suggests it is able to displace other species from a patch. Patches covering up to 40 m^2 occur at several sites suggesting that they have been established for a relatively long period, but satellite plants and patches suggestive of spread by seed were either uncommon or not observed. Presumably patches are expanding slowly, through vegetative propagation, and there is a limit to spread by seed.

3.1.2 Stem Counts

There was no evidence of harvest or other recent disturbances (tree fall or removal, canopy destruction, trampling or vehicle tracks, presence of invading alien species or native species of more open sites, or cutting as indicated by bulldozing, stumps, and log dragging) at any of the 14 populations. There was a five percent increase in the number of stems (557 to 586 stems, Figure 3) between 1998 and 2000 over all quadrat samples combined. Nine out of 14 patches show an increase in the number of stems but the increases are not much larger than the decreases and the average increase per site is only two stems (Figure 4). The greater number of stems in 2000 is due to increases in the number of small stems (Figures 3 and 5). With the exception of Site 2, all patches show either an increase or little decline in small stems, and the increases are much greater than the losses with an average gain of five stems per site (Figure 5). Conversely, almost all patches show either losses or minimal gain in large stems with an average loss of four stems per site and a loss overall (Figures 3 and 6). No seedlings or very small plants ($\leq$ 2.5 cm in leaf width) were noticed, suggesting that stems developed from roots or rhizomes of existing plants, and that effective recruitment by seed was negligible. These data suggest that patches are slowly expanding by vegetative reproduction. Fruiting stems have also increased overall, with only two patches showing a decrease in the fruiting component and an average gain of four fruiting stems per site (Figure 8). However, the increase in fruiting stems was not associated with increased flower production as virtually no change occurred in flowering stems (Figures 3 and 7). The increased number of fruiting stems in 2000 is therefore a result of a greater proportion of flowering stems producing fruit, which may have been a consequence of the weather. No increase in seed production capability actually occurred.

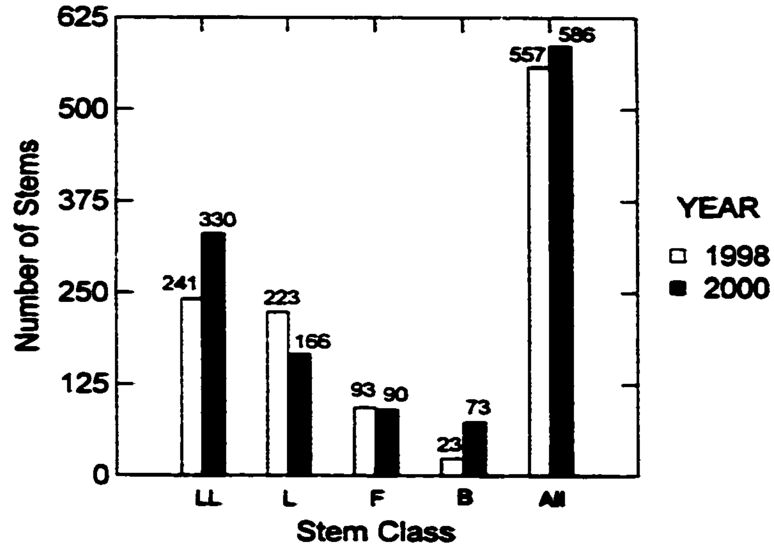

Figure 3. Overall trend in population structure, from 1998 to 2000, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. LL = small non-flowering, L = large non-flowering, F = flowering, and B = Fruiting.

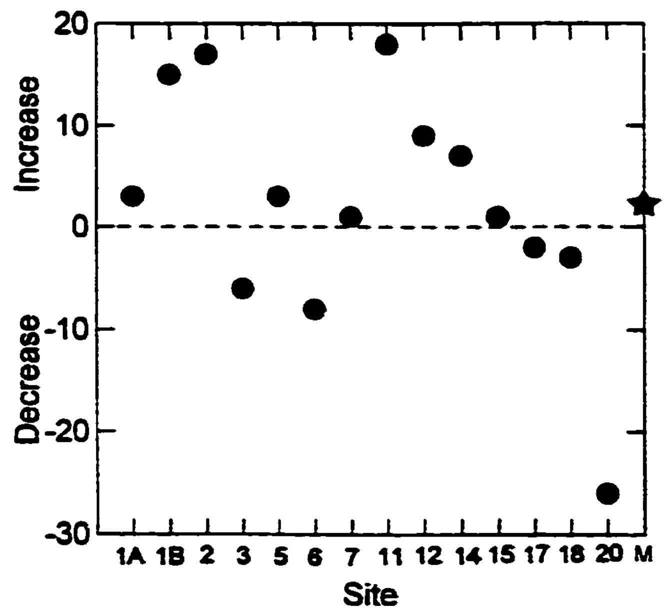

Figure 4. Increases or decreases in total number of stems, from 1998 to 2000, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. M (★) = mean.

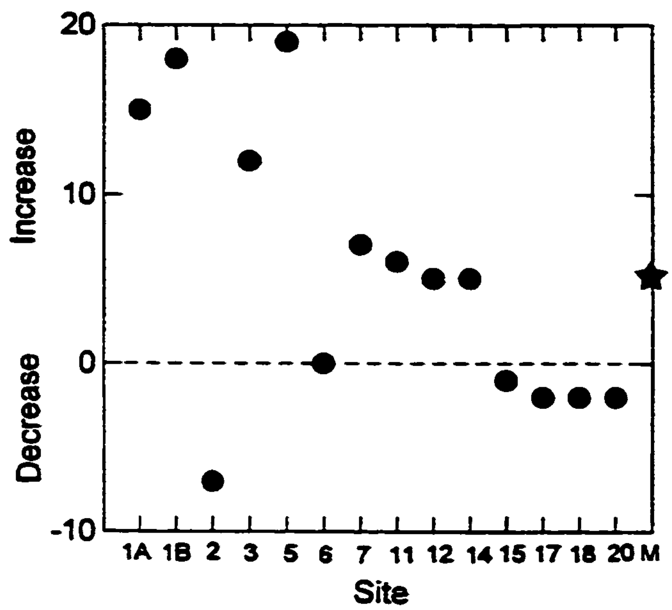

Figure 5. Increases or decreases in number of small stems, from 1998 to 2000, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. M (★) = mean.

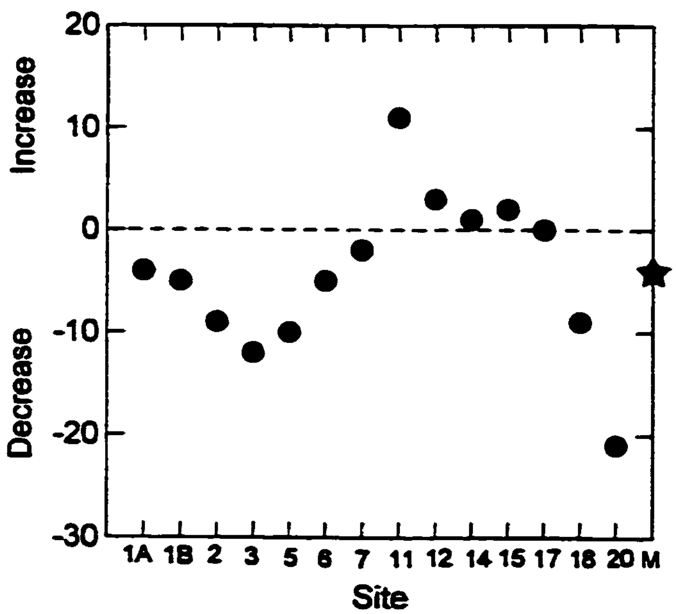

Figure 6. Increases or decreases in number of large stems, from 1998 to 2000, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. M (★) = mean.

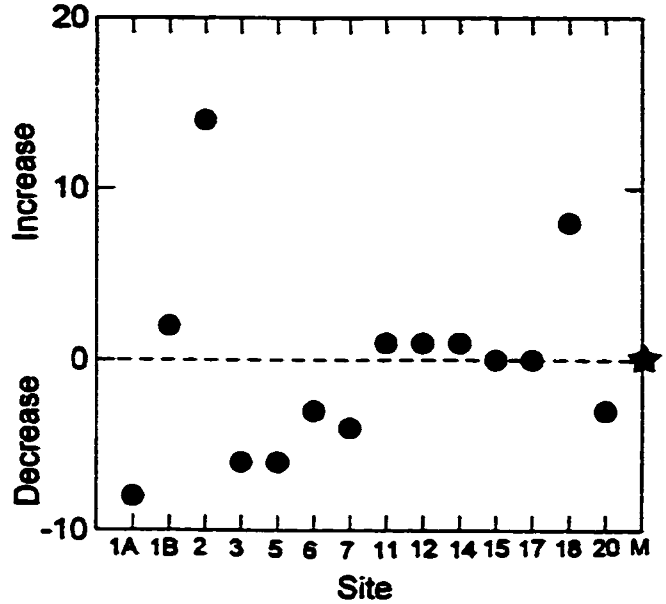

Figure 7. Increases or decreases in number of flowering stems, from 1998 to 2000, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. M (★) = mean.

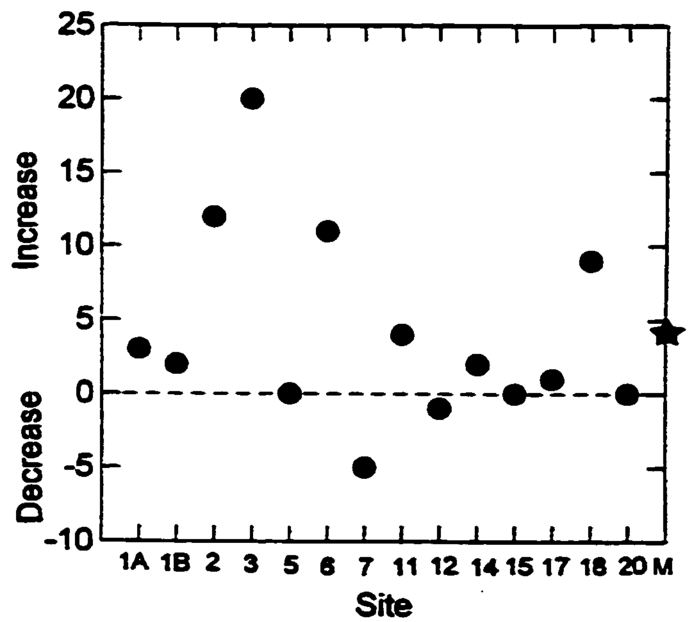

Figure 8. Increases or decreases in number of fruiting stems, from 1998 to 2000, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. M(★) = mean.

The comparison of stem counts, between 1998 and 2000, suggests that goldenseal populations are increasing slightly and slowly. The fact that there was a five percent increase in overall stem production and an increase in fruit production may have been a result of the relatively warmer summers of 1998 and 1999 (Climate Trends and Variations Bulletin for Canada 2001), which are characteristic of the main goldenseal range further south. The minimal increase in stem number supports the survey observations that Ontario populations have not expanded rapidly nor spread substantially over the past few decades and suggests that environmental conditions required for population spread are lacking. The minimal increase is not considered a result of harvest as evidence was not found at any of the populations. The increase in Ontario goldenseal patches correspond to trends in other woodland perennials, such as American ginseng (*Panax quinquefolius* L.) and wild leek (*Allium tricoccum* Ait.), which are slow-growing with population growth rates near equilibrium (population stability or maintenance, Charron & Gagnon 1991, Nault & Gagnon 1993). Evaluation and manipulation of ecological factors that may promote population increase is essential for the recovery of goldenseal from the threatened category.

3.2 Reproductive Ecology - Pollination and Dispersal

3.2.1 Pollination System

None of the four isolated emasculates produced fruit suggesting a requirement of pollination for fruit production. All three plants isolated separately in a natural setting produced fruit, either through insect activity and/or as a result of wind and/or rain, suggesting that plants are self-compatible and pollination can occur in isolated plants. Two of the four hand-pollinated isolated flowers produced fruit, again suggesting at least a degree of selfcompatibility. The other two hand-pollinated isolates may not have produced fruit due to a lack of pollen or stigma maturity at the time of the single pollination event. This evidence, although limited, suggests that pollination is required for seed set.

3.2.2 Pollination and Dispersal

The primary pollinators were small bees, 6-7 mm, referable to the genera *Dialictus* and *Evylaeus* (Table 1). Syrphid flies as well as some larger bees, 8-10 mm long, including an *Andrena* sp., a *Bombus* sp., and *Augochlora pura pura* (Say), also appear to act as pollinators. The small bees are mostly polylectic and thus pollinator specificity seems unlikely. Other studies of vernal woodland herbs have suggested the importance of small bees (Bertin & Sholes 1993) and have also emphasized the importance of a diversity of pollinators (Beattie 1971, Motten 1986).

Since the bees spent up to a minute crawling over an individual flower, the flowers appear to be attractive. The crawling may have involved acquisition of pollen on the surface of the insects, as evidenced by some bees which were covered with goldenseal pollen, that could later be gleaned. This crawling behaviour may represent an adaptation to the prominent stamen cluster morphology of the flower, a morphology shared by other woodland herbs such as dwarf ginseng (*Panax trifolius* L.) and false mitrewort (*Tiarella cordifolia* L.) which were flowering at the same time in some of the sites.

Table 1. Insect visitors (i.e., visiting only one flower) and pollinators (i.e., visiting two or more flowers consecutively) of goldenseal (*Hydrastis canadensis*) at four sites in Essex County, showing both numbers of individuals observed and collected at each site from May 5 to 6, 1999.

Species of Visitors/Pollinators	Amherstburg vis./poll.	Arner vis./poll.	Watford vis./poll	Uttoxeter vis./poll.	Total vis./poll.
Flies					
1. *Eupiodes* sp.		0/1			0/1
2. cf. *Eupiodes* sp.		1/2	0/1	2/0	3/3
Bees					
3. *Andrena* sp., 10 mm long		0/1			0/1
4. *Augochlora pura pura* (Say), 8 mm long	0/1				0/1
5. cf. *Augochlora pura pura* (Say)	2/2	0/2			2/4
6. *Bombus* sp.	0/1				0/1
7. *Dialictus* sp., 6-7 mm long, hairy abdomen, green metallic thorax		0/6	0/2		0/8
8. *Evylaeus* sp., 6 mm long with pure black thorax		0/2	0/1		0/3
9. small bees, 6-7 mm long, probably *Dialictus* and *Evylaeus* sp.	3/3	4/9	1/2	2/2	10/16

At Arner, a large group of at least 50 red-winged blackbirds (*Agelaius phoeniceus* L.) were active within a large patch of 517 plants. One blackbird swooped down, removed a berry and returned to the canopy above. Numerous other birds were flying back and forth, from the canopy to the patch, over a period of about five minutes, and 30 to 50 berries present before the birds arrived were gone after they departed. Other observations of dispersal included rapid disappearance of fruit at all sites with no accumulation on the ground.

Although not extensive, these observations suggest that pollination is not limiting to population growth. Dispersal also appears non-limiting based on the evidence for fruit removal; however, dispersal may be limiting if seeds are not reaching appropriate sites for germination. This type of "non-focussed" dispersal may occur in goldenseal since red-winged blackbirds habit marshes as well as a variety of other habitats such as thickets and shrubs in towns and cities. Thus, the probability of seeds reaching a favourable germination site may be quite low in southwestern Ontario. Other organisms that occur throughout the goldenseal range further south may be more effective dispersal agents including box turtles (*Terrapene carolina* L.), the eastern woodrat (*Neotoma floridana*), and the fox squirrel (*Sciurus niger* L.). Box turtles disperse the yellow fruits of may apple (*Podophyllum peltatum*, L), a woodland herb with morphology similar to goldenseal (Rust & Roth 1981), and in general are known to consume large amounts of berries and to dig and bury in the ground (e.g., Dawson 1999). The woodrat hides its food during the year which consists of herbaceous material including virginia creeper (*Parthenocissus quinquefolia* (L.) Planchon ex DC.), spice bush (*Lindera benzoin* (L.) Blume) leaves and berries, mayapple, jewell-weed (*Impatiens pallida* Nutt.), and grape (*Vitis* sp., Wagle & Feldhamer 1997). The fox squirrel also hides its food and eats a wide variety of fruit, including fruits of osage orange (*Maclura pomifera* (Raf.) C. K. Schneid), mulberries (*Morus* spp.), juniper berries (*Juniperus virginiana* L.), blackberries (*Rubus* spp.), strawberries, and tomatoes (Chapman and Feldhamer 1982).

3.3 Ecological Aspects

3.3.1 Herb, Canopy, and Soil Layer

There was no apparent relationship between either dominant canopy species or soil type and population size, either in terms of number of stems or patches. Large populations of goldenseal occurred in mixed woods dominated by a variety of species, including oaks

(*Quercus* spp.), maples (*Acer* spp.), hawthorns (*Crataegus* spp.), black walnut (*Juglans nigra* L.), cottonwood (*Populus deltoides* Bartr. ex Marsh. ssp. *deltoides*), elm (*Ulmus americana* L.), hickories (*Carya* spp.), ironwood (*Ostrya virginiana* (Miller) K. Koch), basswood (*Tilia americana* L.), and ashes (*Fraxinus* spp., Tables 2 and 3). However, a relationship between occurrence or population size of goldenseal and canopy composition may have been found had a quantitative mapping approach been taken. There was no evidence of grazing mammals found at any of the goldenseal sites. All populations occurred in loamy soil, either loam, sandy loam, or clay loam, and both large and small populations, based on stem number or patch size, occurred in the same type of soil (Tables 2 and 3). Multiple linear regression, using either backward or forward stepwise procedure, revealed no significant relationships between the environmental variables and the number of stems, in each size class or overall. There was a significant positive relationship between the number of small (young) stems and phosphorus; however, significance was due to a single site with the highest concentration of phosphorus (an outlier in the analysis). A larger number of soil samples that are dried on site, to avoid errors in results attributed to transporting moist soil in bags, would improve the evaluation of soil effects. Nonetheless, according to fertility guidelines for native ornamentals (OMAFRA 2000), all populations occurred in soil with high organic matter, high calcium, and adequate magnesium, manganese, and zinc. Conversely, all but one population occurred in soil with low phosphorus. The one population in soil with a moderate amount of phosphorus was the one with the highest number of young stems. This suggests that phosphorus may be a limiting factor.

Table 2. Site characteristics for 13 goldenseal populations near northern range limit in Ontario: number of stems and patches, number of stems in quadrat sample (Qstems), dominant canopy species, soil pH, nutrients (ppm), organic matter (OM, % dry weight), and soil type (L = loam, SL = sandy loam, CL = clay loam). Soil samples were taken from quadrats within which goldenseal grows. Soil texture is based on estimates from sample and consideration of local soil survey data. A = Ash (*Fraxinus* sp.); C = Cottonwood (*Populus deltoides* Bartr. ex. Marsh. ssp. *deltoides*); Hs = Shagbark Hickory (*Carya ovata* (Miller) K. Koch); Hb = Bitternut Hickory (*Carya cordiformis* (Wangenh.) K. Koch); I = Ironwood (*Ostrya virginiana* (Miller) K. Koch); M = Maple (*Acer* sp.); Msu = Sugar Maple (*Acer saccharum* Marshall); Or = Red Oak (*Quercus rubra* L.); W = Black Walnut (*Juglans nigra* L.).

Stems	1153	768	106	4329	45	2324	2597	455	188	440	37	241	648
Patches	8	10	1	3	1	2	8	2	2	3	1	1	4
Qstems	18	55	50	75	31	50	41	51	6	52	15	41	92
Canopy	Hs	W	I	Or, I	C	I, A	Hs, Or	Msu	Msu	M	Msu	Hb	A
pH	6.3	6.4	7.5	6.3	6.1	6.1	5.7	5.4	5.7	7.8	7.4	7.8	7.3
P (ppm)	14	8	9	7	10	12	12	11	11	14	12	7	30
K (ppm)	140	176	179	100	149	93	123	72	73	141	230	77	114
Mg (ppm)	266	323	528	300	290	221	375	114	100	257	191	169	203
Ca (ppm)	2270	2780	8240	2730	2420	2360	2710	1290	1420	7350	8300	6960	3990
Mn (index)	30	22	16	20	25	24	38	42	33	18	16	17	17
Zn (index)	27	43	26	26	29	60	48	30	33	29	36	18	30
OM (%)	9.7	8.9	12.1	8.2	8.1	9.4	11.1	5.8	5.9	13.5	23.1	10.7	6.9
Soil Type	CL	CL	SL	L	SL	SL	CL	CL	SL	SL	SL	CL	CL

Table 3. Site characteristics for seven goldenseal populations near northern range limit in Ontario for which soil samples were not available: number of stems and patches, number of stems in quadrat sample (Qstems), dominant canopy species, and soil type (SL = sandy loam). Soil texture characteristics are based on local soil survey data. A = Ash (*Fraxinus* sp.); Bas = Basswood (*Tilia americana* L.); E = Elm (*Ulmus americana* L.); Haw = Hawthorn (*Crataegus* sp.); Mr = Red Maple (*Acer rubrum* L.); Ms = Silver Maple (*Acer saccharinum* L.); Ob = Bur Oak (*Quercus macrocarpa* Michx.); Or = Red Oak (*Quercus rubra* L.).

Stems	283	165	640	203	45	261	10
Patches	2	5	7	5	1	1	1
Qstems	73	45	70	30	36	123	7
Canopy	E, Bas	Haw	Ob, Bas	Mr, Or	Haw	Haw	Ms
Soil Type	SL	SL	SL	SL	SL	SL	SL

3.3.2 Habitat Size

There was no significant linear relationship between natural area size and either number of goldenseal stems ($P = 0.982$, $R^2 = 0.000$) or patches ($P = 0.926$, $R^2 = 0.001$). There was a significant negative relationship between habitat size and number of stems ($P = 0.040$, $R^2 = 0.213$, Figure 9). Conversely, there was no significant relationship between habitat size and number of patches ($P = 0.126$, $R^2 = 0.125$). Removal of the largest, and possibly less well explored natural areas, failed to provide an indication of a significant relationship between natural area size and number of stems ($P = 0.385$, $R^2 = 0.076$) or patches ($P = 0.626$, $R^2 = 0.025$). Thus, goldenseal population size is unrelated to size of the entire natural area but relatively larger populations occur in smaller habitats.

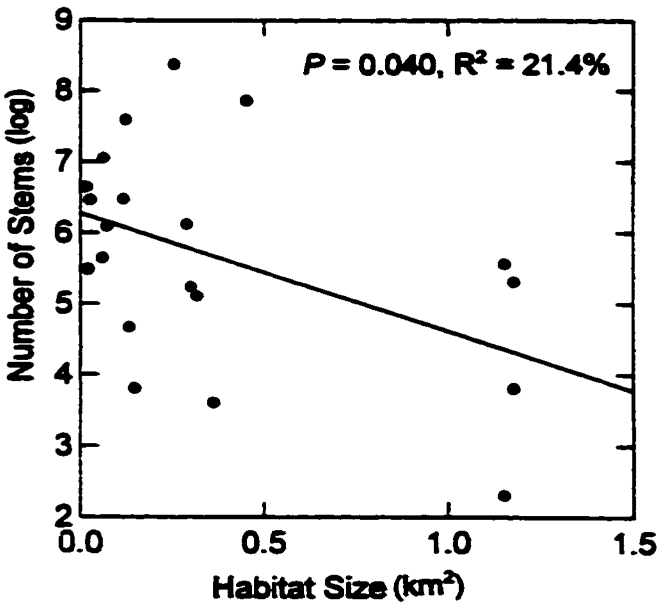

Figure 9. Number of stems (log) within 20 goldenseal populations in Ontario plotted against habitat size (km^2).

The results suggest that goldenseal may be adequately protected in relatively small areas supporting the view that small areas are worthy of serious consideration for species conservation (e.g., Higgs & Usher 1980, Järvinen 1982, Reznicek 1987). Reznicek (1987) explains the basis for this in depth by outlining differences between plants and animals, noting long lifespan and seedbank, inbreeding capability, fit in small areas, and use of a single habitat. The data are considered a reliable suggestion of minimal area effects since none of the sites have been substantially reduced in size over the past few decades. To the extent that small habitats may be more disturbed due to increased edge effects, the data suggest that goldenseal may be promoted by disturbance. However, edge effects on plants may not be more pronounced in small woodlots (Burke & Nol 1998). Regardless, a beneficial effect of large natural areas or habitats is not supported and the results are contrary to expectation for a species assigned the high conservatism score of 8 (floristic quality index for southern Ontario) based on its fidelity to unaltered or undisturbed habitats (Oldham *et al.* 1995, Francis *et al.* 2000).

3.3.3 Spatial Analysis of Goldenseal Occurrence

There were no expected or observed goldenseal points near paths for 11 sites. For the remaining nine, goldenseal occurrence near paths was greater than expected at each site, and in three of these sites it was significantly greater (Table 4). For seven of 13 sites, with expected frequency exceeding zero, goldenseal occurrence near edges was greater than expected, and in three of these sites it was significantly greater (Table 4). Overall, there was a significantly greater association of goldenseal points with both paths ($P = 0.004$) and edges ($P = 0.015$). Although the aim has been for an objective and statistically appropriate consideration of the question of the effect of disturbance, an association would be a compelling conclusion with seven of the 20 known sites having goldenseal plants within 10 cm of the compacted and bare portion of paths and sometimes even in the middle of the path.

Of the total 75 goldenseal points at all sites, 24 were near paths and 35 were near edges (Table 4). Significantly increased frequency near paths ($P < 0.0005$) and edges ($P < 0.0001$) with regard to expectation, based on the total number of points, suggests a beneficial effect of both. The strong indications of a positive relationship of goldenseal with paths and edges is assumed to be a consequence of associated disturbance to soil and/or canopy (increased light), but the effect may also be indirect and mediated by dispersal, pollination, or other phenomena.

Table 4. Site numbers, habitat sizes (km^2), natural area sizes (km^2), number of goldenseal stems (ramets), number of goldenseal patches (G points), number of neighbourhood points (N points), Chi-square for paths and edges (Yates corrected) and associated significance level (*P*) for 20 sites in southwestern Ontario. Sites with the same number of asterisks (*) indicate shared natural areas.

Site	Habitat Size (km^2)	Natural Area Size (km^2)	Number of Stems	G Points	Path G Points	N Points	Path N Points	Path Chi-sq.	*P*	Edge G Points	Edge N Points	Edge Chi-sq.	*P*
1A*	0.062	0.101	1153	8	4	43	10	1.50	0.221	0	6	0.34	0.600
1B*	0.017		768	11	0	22	0	0		11	22	0	
2	0.131	0.135	106	1	0	19	8	0.02	0.888	0	3	0.72	0.396
3	0.254	0.291	4400	9	5	90	16	5.26	**0.022**	0	0	0	
4	0.146	0.110	45	1	0	8	0	0		0	0	0	
5	0.121	0.751	1980	1	1	25	6	0.28	0.597	0	0	0	
6	0.452	0.488	2597	9	2	55	3	2.45	0.118	5	7	9.48	**0.002**
7	0.289	0.592	455	3	0	40	9	0.06	0.806	0	3	0.32	0.600
8	0.059	0.079	283	5	3	40	6	4.63	**0.031**	4	10	4.05	**0.044**
9	0.316	0.359	165	2	0	42	0	0		14	42	0	
10	0.026	0.270	640	6	0	33	0	0		3	7	1.22	0.269
11**	1.175	2.536	203	3	0	34	0	0		0	5	0.01	0.920
12**	1.175		45	1	0	15	0	0		1	5	0.09	0.764
13**	1.150		261	1	0	20	0	0		0	0	0	
14**	1.150		10	1	0	15	0	0		0	0	0	
15	0.300	0.521	188	2	2	28	6	2.78	0.095	0	0	0	
16***	0.071	4.574	440	3	3	49	10	6.02	**0.014**	3	9	6.91	**0.009**
17***	0.363		37	2	0	24	0	0		0	0	0	
18	0.022	1.996	241	1	1	25	6	0.28	0.597	1	3	1.20	0.273
20	0.115	0.901	648	5	3	11	2	2.84	0.092	5	7	0.53	0.467

4. Conclusions

Goldenseal populations do not appear to be spreading but expanding slowly through vegetative reproduction. Population increase does not seem limited by pollination and conditions required for spread do not seem to be related to soil type or plant associates in the herb and canopy layers. Population increase may be limited by "non-focused" dispersal since the apparent dispersal agents likely do not spread seeds at appropriate germination sites. Increase in goldenseal may be disturbance-dependent since occurrences of goldenseal have been associated with disturbance and populations of plants in disturbed habitats, where more resources such as light and nutrients are made available, tend to expand rapidly (e.g., *Pedicularis furbishiae* S. Wats. and *Danthonia sericea* Nutt, Gagnon 1999). Additional support for a positive disturbance effect includes the lack of association of large population size with both natural area and habitat size. The low concentration of available phosphorus in the soil where goldenseal occurs, and the largest number of young stems at one site with the highest concentration of phosphorus, further lend support to a positive disturbance effect especially with consideration of the loss of fertilization events by passenger pigeons (bird droppings are high in phosphorus, see Centre Européen d'Études des Polyphosphates 2002). The evidence for a positive disturbance effect supports an experimental test of the hypothesis, proposed based on the review of disturbance ecology (Section 1.4.4), that goldenseal will benefit from simulation of natural disturbance to the forest floor.

Part II: Experimental Test of Disturbance as a Limit to Population Growth

5. Materials and Methods

5.1 Study Area

The study was carried out at five of the goldenseal sites. Four sites occur near the town of Arner (42° 02′ N, 82° 49′ W in Gosfield South Tp. of Essex County) and one near the town of Amhertsburg (42° 06′ N, 83° 06′ W in Malden Tp. of Essex County). Exact locations are not given for conservation reasons but are maintained as a confidential file by the Chairman of the Subcommittee for Plants, Committee on the Status of Endangered Wildlife in Canada (COSEWIC).

5.2 Experimental Design

A random block experiment, for both seeds and transplants, was set out to test the effects of substrate disturbance on goldenseal growth and reproduction (Figure 10). Twenty 3 x 3 m blocks at each of five sites for transplants, and ten 3 x 3 m blocks at each of four of these sites for seeds, were randomly placed throughout apparent goldenseal habitat (within 30 m of existing colonies), permanently marked with aluminum pins and tags, and mapped. Sites with large populations were chosen so that the effect of manipulation on the populations would be minimized.

One day prior to sowing seeds or transplanting, four treatments were randomly applied to each block. Each treatment covered 1 m^2 and was 1 m apart in each block to avoid effects of neighbouring plots. Treatments consisted of: (1) substrate turnover, in which the ground was overturned to 4 cm depth with a shovel; (2) fertilization, in which 7 g of slow release granular bone meal (2:14:0 NPK) was evenly sprinkled directly over the ground; (3) both substrate turnover and fertilization; and (4) control (no manipulation). The substrate disturbance treatment theoretically resembles upheavals created by massive floods or the digging by large extirpated or extinct mammals or erosion following death of flora due to grazing, fertilization event, etc. The fertilization treatment fulfills requirements for field nursery stock based on soil tests (OMAFRA 2000), and assumes loss of fertilization events resulting from floods or formerly present fauna, including for example, flocks of passenger pigeons (*Ectopistes migratorius* L.). Only two levels of nutrients and disturbance were used due to limited time, restricted habitat area, and inadequate population size (undesirable to involve more than 10 percent of the population in experimental manipulation).

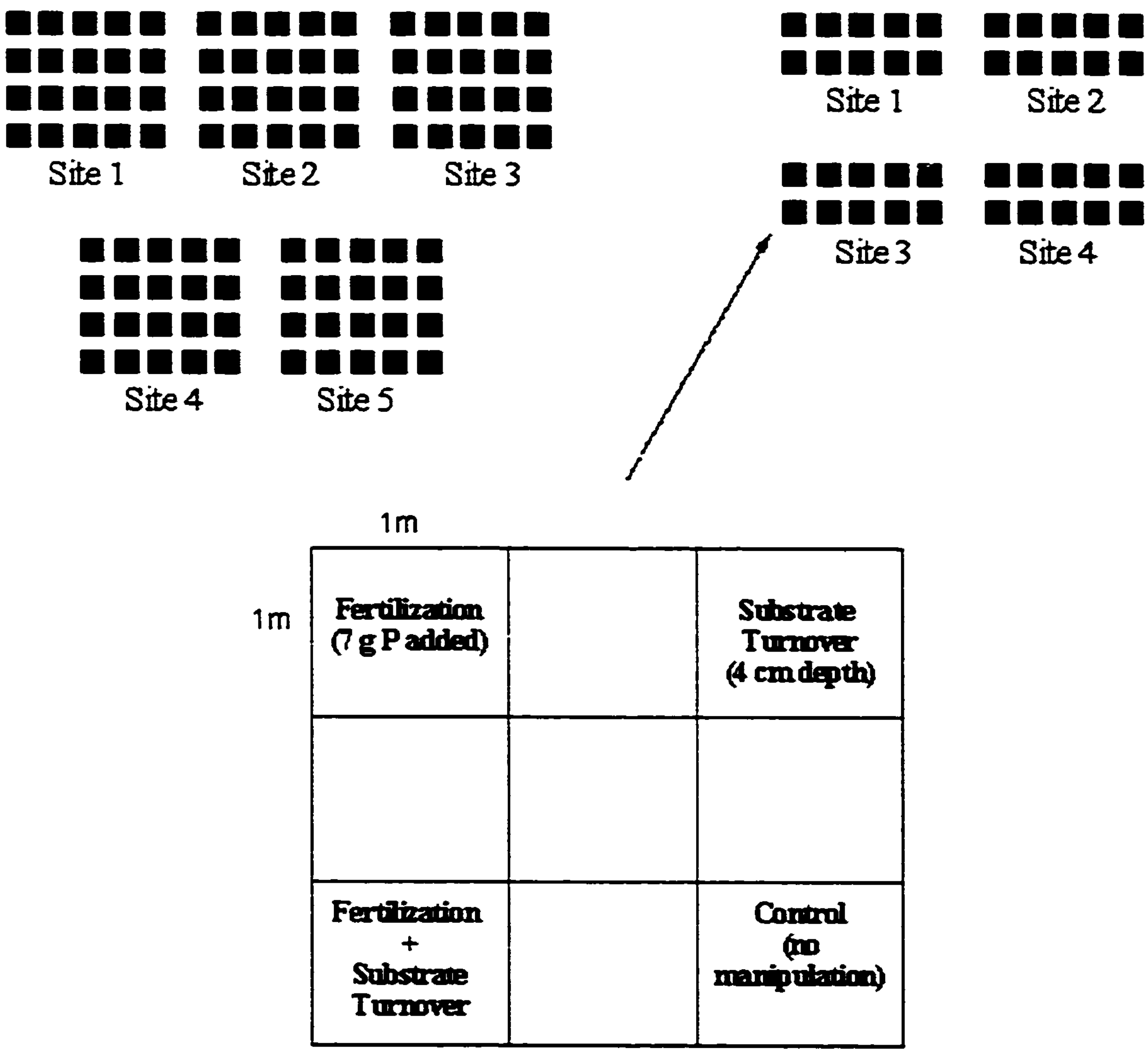

Figure 10. Random block experiment with four treatments: (1) fertilization, in which 7 g of slow release granular bone meal (2:14:0 NPK) was evenly sprinkled directly over the ground; (2) substrate turnover, in which the ground was overturned to 4 cm depth with a shovel; (3) both substrate turnover and fertilization; and (4) control (no manipulation). Twenty blocks at each of five sites used for transplanted rhizomes. Ten blocks at each of four of these sites used for seeds.

5.3 Seed Planting

From July 11 to 15, 1999, using rubber gloves, fully ripe fruit were picked from nearby colonies, squashed, and the seeds separated. In the 10 blocks set out for seeds at each of the four sites, 25 seeds were placed just below the substrate surface along a 7″ grid within each of the four treatment plots. This grid was chosen based on cultivation literature (e.g., Davis 1996) in order to maximize the number of seeds per plot. Planting seeds in an orderly fashion enables each seed to have an approximately equal chance of germinating and facilitates following their fate through knowledge of their positions.

5.4 Transplanting

From August 24 to 27, 1999, at start of senescence, rhizomes from stems that had flowered or lost fruit were transplanted from nearby colonies, with gloves and a trowel, into the centre of each 1 m^2 treatment plot in the 20 blocks set up for transplants at each of the five sites. Stems that had flowered and/or fruited were chosen to eliminate life stage as a factor and to ensure rhizomes of approximately equal size with approximately equal capability to produce biomass, flowers, and fruit the following year. Variability in rhizome size was accounted for by measuring the length and width of rhizomes before transplanting.

5.5 Data Collection

From May 4 to 6, June 19 to 21, and August 21 to 23, 2000, and from May 7 to 9 and July 9 to 12, 2001, stem height (cm) and leaf width (cm) of transplants were measured. Presence or absence of flowers and fruit were noted in 2000 and the number of pericarp divisions per transplant fruit were counted as an estimate of seed production (to avoid squashing fruit and interfering with dispersal) in 2001. Pericarp divisions were not counted in

2000 due to sporadic fruiting within and between sites (berries did not develop at the same time). Although fruiting is a more direct measure of recruitment capability than simply flowering, both provide a better indication due to the possibilities that: (1) flowering is limited by pollination, although preliminary evidence suggests otherwise (Section 3.2); (2) some stems may be lost between flowering and fruiting; and (3) fruits may be removed before counting even though fruits were measured before they were ripe. Seedling tops were visible in 2001 and the number of seedlings in each treatment plot was recorded from May 9 to 12.

Cover (as an index of biomass production) was estimated as the maximum surface area of photosynthesizing structures (leaves, stems, flower buds, and pre-mature fruit) attained over the growing season. This was calculated as the sum of the area of the upper leaf surface (πr^2), stem area ($2 \pi r h$, using an estimated radius of 0.15 cm), bud area (πr^2, using an estimated radius of 0.5 cm), and pre-mature fruit area (πr^2, using an average fruit radius of 0.6 cm based on the width of 60 fruit, 3 selected randomly from each of 20 populations). Rhizome size was calculated as volume ($\pi r^2 h$).

In order to account for the influence of light, measurements were taken under a full canopy and cloudless sky on September 29 and 30, 2001, between 11 am and 3:30 pm. Photosynthetically active radiation (PAR, expressed in $\mu E/cm^2 sec$) reaching plant height was measured in the centre of each block using a handheld quantum sensor (LI-190S, LI-COR, Inc., Nebraska, USA). Measurements were taken while blocking out direct sunlight, or sunspots, by casting a shadow on the sensor with a piece of cardboard (21.3 cm x 27.5 cm) held approximately 1.5 m above the sensor. This method provided an indication of the average light in the area of the block. Although direct sunlight was not accounted for, it is related to average light because average light increases with openings in the canopy through which direct sunlight penetrates. It was impractical, given the number of blocks, to include sunspots since they move with both time and canopy motion. Several hours of recording would have been required to obtain an accurate average.

Thus, for transplants, data include initial rhizome size (cm^3), total area of photosynthetic surface (cm^2) and number of flowers and fruit in 2000 and 2001, as well as number of seeds per fruit in 2001, in each of four treatments (substrate turnover, fertilization, substrate turnover + fertilization, control), in each of 100 blocks over five sites. For seeds, data include number of seedlings and occurrence of germination in each of the four treatments, in each of 40 blocks over four sites.

5.6 Statistical Analysis

Since some of the transplanted rhizomes did not produce a stem and some of the seeds did not germinate, one-way analysis of variance (ANOVA) was used to determine the relationship between treatment and lack of stem and seedling production. Either rhizomes and seeds had died or were dormant because conditions were poor. The analysis was necessary to validate the assumption made in subsequent analyses of treatment effects on biomass, fruit, seed, and seedling production, that there is no differential effect of treatment on stem and seed production.

Nonparametric multiway analysis of variance (ANOVA), by an extension of the Kruskal-Wallis test, was used to examine the effect of treatment, site, and block nested within site, as well as the covariable light, on the goldenseal response variables, including biomass, flower, fruit, and seed production as well as the number of seedlings and occurrence of germination. Nonparametric methods were used because the response variables were either highly variable and/or highly discontinuous causing violation of the assumptions for parametric analyses. Nesting block within site was appropriate because the experiment involved subgroups (blocks) within samples (sites) and nesting enabled appropriate partitioning of error. Multivariate methods were not necessary since there were few cases of correlation that were considered high among the response variables (i.e., $r_s > 0.70$, Table 5). Differences between treatment means were examined using nonparametric Tukey-type multiple comparisons (Zar 1984) and the hypothesis was one-tailed in each case. One-tailed p values were obtained by dividing the resulting p value in half if the difference between group means was consistent with the alternative hypothesis, or by dividing the resulting p value in half and subtracting this value from one, if the difference was inconsistent with the alternative hypothesis. Spearman's rank correlation procedure was used to further elucidate the relationship of light (PAR) with the goldenseal response variables since the assumptions for linear regression were violated due to highly discontinuous data.

Table 5. Spearman's rank correlation coefficients, relating goldenseal biomass, flower, and fruit production in 2000 and 2001 as well as seed production in 2001. Significance is not provided since sample size was very high in each case (i.e., > 390).

	Variable X					
Variable Y	biomass 2000	flowers 2000	fruit 2000	seeds	biomass 2001	flowers 2001
biomass 2000						
flowers 2000	0.483					
fruit 2000	0.533	0.759				
seeds per fruit	0.272	0.217	0.255			
biomass 2001	0.629	0.269	0.339	0.457		
flowers 2001	0.494	0.186	0.272	0.790	0.494	
fruit 2001	0.266	0.191	0.228	0.986	0.466	0.804

6. Results

The ANOVAs involving lack of stem production (rhizome death or dormancy) and treatment revealed no significant effect of treatment, in either the first ($P = 0.926$, $R^2 = 0.001$) or second year ($P = 0.998$, $R^2 = 0.000$, Appendix B). Eighty-five percent of the 400 transplants survived and produced one or more stems in 2000 and 70% survived in 2001. The percentage survival varied from 74 to 91% over the five sites in 2000 and from 67 to 95% the following year. In 2000, 24 to 53% of the transplants produced flowers, depending on the site, with 39% flower production overall. Twenty to 41% produced fruit with 32% fruit production overall. In 2001, 23% of the 340 surviving transplants produced flowers and 16% produced fruit, ranging from 14 to 37% and 7 to 31% over the five sites, respectively. Germination occurred in 52 of the treatment plots (in 26 blocks) and ranged from 2.6 to 3.9% over the four sites with 3.4% germination overall (134 of the 4000 seeds). Based on the ANOVA, treatment did not have a significant effect on lack of germination (seed death or dormancy, $P = 0.773$. $R^2 = 0.007$, Appendix B).

Despite a potential interaction with treatment, the influence of rhizome size was not considered because rhizome size did not differ significantly between treatments ($P = 0.803$, $R^2 = 0.002$, Appendix B). There were no significant interaction effects of treatment and site on any of the goldenseal variables (Appendix B) and since biologically significant differences between sites were not elucidated, variations in flower, fruit, and seed production, as well as germination, due to site were not pursued. As anticipated, there was a significant interaction effect of site and light because sites differed substantially in canopy cover. Light effects are discussed below.

6.1 Biomass

Disturbance simulation increased the production of biomass in both years (Figure 10a). After one year, rhizomes in plots with soil turnover produced the greatest amount of biomass, followed by rhizomes in soil turnover + fertilization, fertilization, and control plots. There was significantly more biomass in soil turnover plots compared to the control ($P < 0.05$). After two years, soil turnover + fertilization plots had the most biomass followed by soil turnover, fertilization and the control. The increase in biomass in the fertilization + soil turnover treatment in the second year was much greater compared to the other treatments. Although differences between the soil turnover treatments (T and FT, Figure 11a) and the control were not statistically significant in the second year based on the Tukey-type multiple comparison test, they may be biologically significant given the fact that the power of the ANOVA test was low ($1 - \beta = 0.34$). Power was not high enough to detect an effect with a 66% chance of accepting a false null hypothesis of no difference between treatment means. Thus, in both years, treatments involving soil turnover, with or without fertilization, had the greatest effect on biomass production.

6.2 Flower Production

Disturbance simulation increased the production of flowers in both years overall (Figure 11b). Although the amount of variation was quite small in 2000, flower production was highest in plots with soil turnover, followed by fertilization, control, and soil turnover + fertilization plots. In the second year, flower production mirrored biomass production, with the highest flower production in plots with soil turnover + fertilization, followed by soil turnover, fertilization and control plots. The soil turnover and soil turnover + fertilization treatments had significantly more flowers compared to the control treatment after two years ($P < 0.05$, Figure 11b). The soil turnover + fertilization treatment also had significantly more flowers compared to the fertilization treatment ($P < 0.05$, Figure 11b).

6.3 Fruit Production

Similar to first year flower production, fruit production was highest in plots with soil turnover but approximately the same in the other treatments. In the second year, fruit production also mirrored biomass production, with the highest fruit production in plots with soil turnover + fertilization, followed by soil turnover, fertilization and control plots. The soil turnover and soil turnover + fertilization treatments had significantly more fruit ($P < 0.005$) compared to the control treatment after two years (Figure 11c).

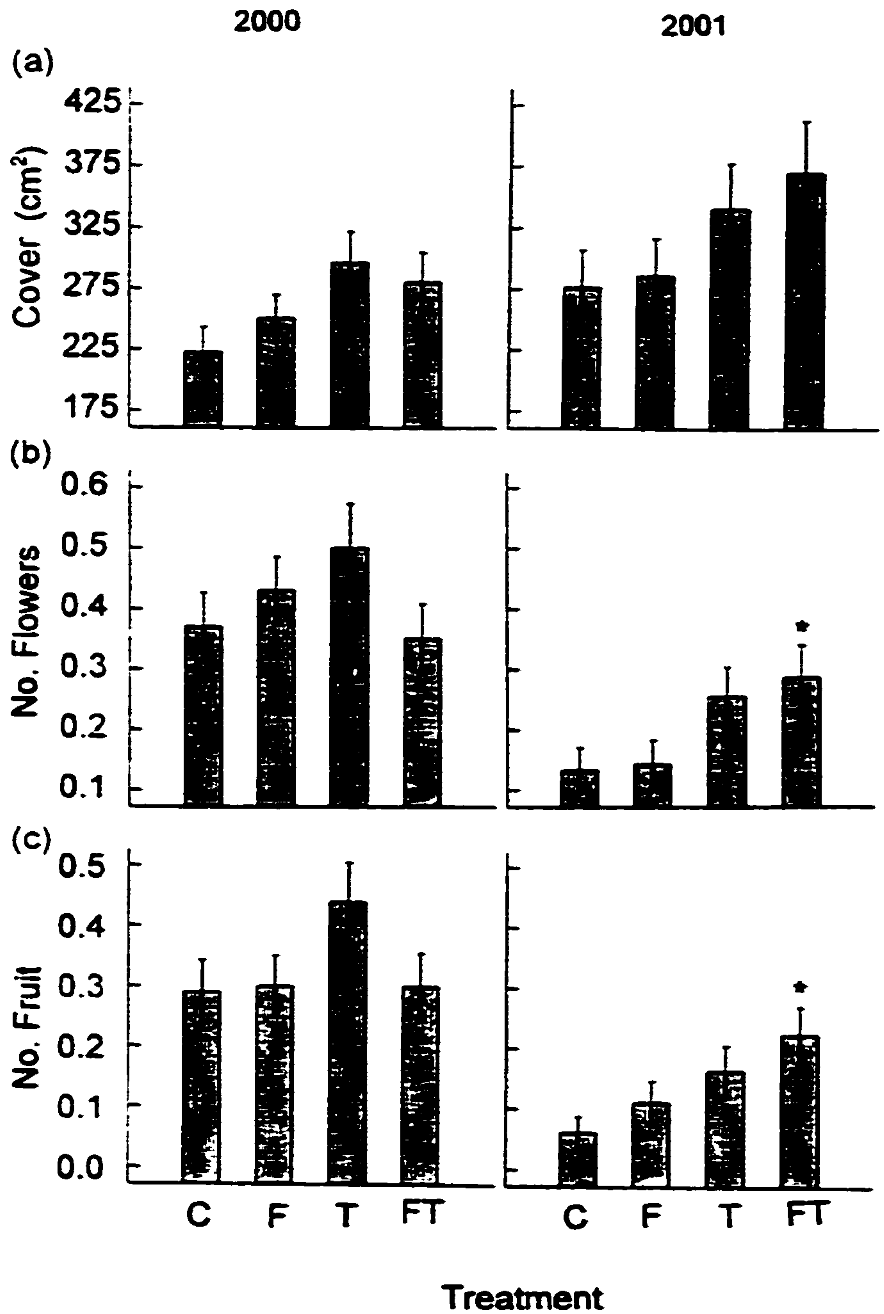

Figure 11. Mean (a) cover (cm^2), (b) flower production, and (c) fruit production of goldenseal in four treatments (C = control, F = fertilization, T = soil turnover, FT = fertilization + soil turnover) at the end of 2000 and 2001 growing seasons. Solid bars represent means and vertical lines represent standard errors. Asterisks (*) indicate $P < 0.05$ (one-tailed) compared to the control. N = 100.

6.4 Seeds

Seed production corresponded to biomass production, with the highest seed production in plots with soil turnover + fertilization, followed by soil turnover, fertilization and control plots. The soil turnover + fertilization treatment had significantly more seeds ($P < 0.01$) compared to the control treatment after two years (Figure 12a). The significant increase in the production of seeds, associated with disturbance simulation, was not accompanied by significant increase in germination and number of seedlings. Disturbance simulation did not have a significant effect but there was a great amount of variation within treatments (Figure 12b,c).

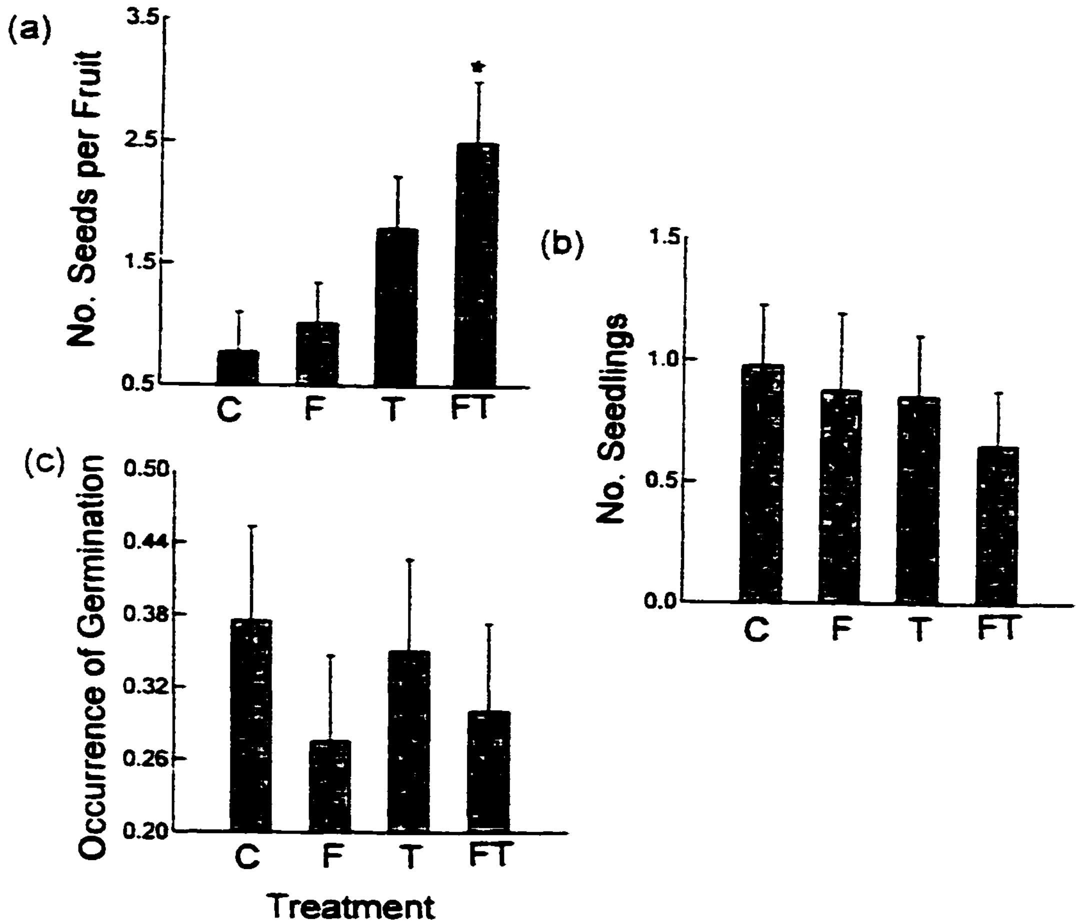

Figure 12. Mean (a) number of seeds per fruit (N = 100), (b) number of seedlings (N = 40), and (c) occurrence of germination (N = 40) of goldenseal in four treatments (C = control, F = fertilization, T = soil turnover, FT = fertilization + soil turnover) at the end of 2001 growing season. Solid bars represent means and vertical lines represent standard errors. Asterisk (*) indicates $P < 0.05$ (one-tailed) compared to the control.

6.5 Light

Second year biomass production was significantly correlated with light, with more biomass produced under higher light ($P < 0.002$) but only about two percent of the variability in biomass was explained by the correlation (Table 6). The positive correlation between biomass and light in the second year contrasts with the slightly negative and minimal correlation between light and biomass production in the first year. There was no significant interaction effect of light and treatment on biomass production in either the first or second year (Appendix B). Flower production was positively correlated with light, but only in the second year, and both the significance ($P = 0.05$) and explained variability were low (0.8%, Table 6). There was no significant interaction between light and treatment on flower production, in either the first or second year. Second year fruit production was significantly correlated with light, with more fruit produced under higher light ($P < 0.005$) but again, explained variability was low (2%, Table 6). Based on the ANOVA, there was a significant interaction between light and treatment ($P < 0.03$). Separate correlation procedures for each treatment showed that more fruit was produced under higher light in each treatment, but the correlation was only significant in the soil turnover treatment ($r_s = 0.2835$, $0.002 < P < 0.005$). Seed production was also significantly correlated with light, with more seeds produced under higher light ($P \ll 0.005$), but there was no interaction effect of treatment and light (Appendix B). The number of seedlings and the occurrence of germination were positively correlated with light ($P < 0.001$ in both cases), and although explained variability was again low (approximately 9% in each case), much more was explained by these correlations compared to those with the other goldenseal response variables.

Table 6. Spearman's rank correlation coefficients (r_s) and significance (*P*), relating photosynthetically active radiation (PAR) to response of goldenseal, including biomass, flower, and fruit production after the 2000 and 2001 growing seasons as well as seed production, number of seedlings, and occurrence of germination after the 2001 growing season.

	Variable X	
	PAR	
Variable Y	r_s	*P*
biomass in 2000	0	> 0.500
biomass in 2001	0.156	**< 0.005**
no. flowers in 2000	-0.1	> 0.100
no. flowers in 2001	0.09	**0.05**
no. fruit in 2000	0	> 0.500
no. fruit in 2001	0.151	**< 0.005**
no. seeds per fruit	0.152	**< 0.005**
no. seedlings	0.301	**< 0.001**
germination	0.29	**< 0.001**

7. Discussion

7.1 Transplanting and Planting Seeds

Transplanting goldenseal, within 30 m of existing colonies in the apparently appropriate habitat, can be used to effectively recover goldenseal. The use of rhizomes, although sometimes unsuccessful with poor site preparation (Hurkmans 1995), may be more effective than attempts at recovery from seed, with 85% overall survival in the first year and 70% in the second less favourable year (dry and hot), as well as production of flowers and fruit. This level of mortality may be considered high in comparison with transplanted bulbs of wild leek (*Allium tricoccum* Ait.) which, in poor habitats, produced progressively smaller leaves over five years before dying (Vasseur & Gagnon 1994). However, bulbs may have greater reserves to withstand transplanting shock and/or poor conditions and greater protection against damage in a transplanting operation is afforded to buds by bulbs compared to rhizomes. Although the new seedlings represent 26 out of 160 potential new patches (each experimental block is considered a new patch), the transplanted rhizomes represented 99 new patches out of 100 potentials in 2000 and 95 new patches at the end of 2001. Furthermore, the overall percentage of seeds that germinated was very low (3.4%, 134 out of 4000 seeds) and other experiments involving sowing seeds of rare and extirpated woodland perennial plants have shown that establishment may be difficult even if the site is experimentally disturbed to enhance the probability of colonization (Primack 1996). However, since seeds are potentially a result of genetic crossover (if not all stems in a population belong to the same clone), sowing seeds should not be completely disregarded as this action may prove valuable in terms of long-term recovery. Since area of occupancy and area of occurrence of goldenseal are both increased, two criteria relating to recovery, in terms of transferring a species to a lower risk category, are directly addressed (Hilton-Taylor 2000, Catling 2001a, Appendix A). If there is a sufficient number of plants in the population to allow transplanting and if sites within the apparent habitat can be manipulated to promote spread in the longer term, conservation value of transplanting rhizomes would be enhanced. This type of "local" transplanting may prove advantageous over augmentation using propagules grown *ex situ* in terms of adaptation to local habitat conditions, maintenance of the genetic structure, and value of the existing natural habitat.

7.2 Disturbance Simulation

Results show that substrate disturbance benefits goldenseal. The increased biomass with substrate disturbance in both years provides an opportunity for increased reproduction by either root tips, rhizome buds, or seeds. The much greater increase in biomass in the fertilization + soil turnover treatment in the second year, in relation to the other treatments, may be attributed to a greater ability to assimilate increased nutrients from the disturbance treatment, as a result of the time required to re-develop an adequate root system after transplanting. An additive effect of fertilization + soil turnover (i.e., 2 x or more the effect of either treatment alone) was not observed possibly due to a maximum limit in the ability to produce biomass, flowers and fruit or the fact that soil turnover causes a release in nutrients, and therefore, a similar effect. Statistical significance may not have been achieved due to the amount of variability beyond the control of the field experiment due to various aspects including the use of wild genotypes as well as differences in environmental conditions and ecological factors. In contrast, higher levels of significance are often achieved in standard agronomy experiments, where plants of the same cultivar are grown in the same conditions. Despite the much reduced fecundity in the second year, the significant increase in flowers and fruit associated with soil turnover and soil turnover + fertilization as well as the significant increase in seeds associated with the fertilization + soil turnover treatment supports the suggestion of increased biomass contributing to increased reproduction. Flowering and fruiting may have been less in the second year due to the unusually dry and hot weather. The year 2001 was the fourth warmest and 12th driest year on record in the Great Lakes - St. Lawrence Region since 1948 (Climate Trends and Variations Bulletin for Canada 2001).

The lack of significant effect of disturbance simulation on number of seedlings and occurrence of germination may also be attributed to drought conditions, possibly in combination with site effects. Specifically, light may have influenced the results, as more seedlings occurred under higher light but not all experimental plots occurred in high light. Substrate disturbance may have promoted germination of goldenseal if all treatment plots were placed in high light. Similarly, in the case of the northern downy violet (*Viola fimbriatula* Sm.), the increased germination reported may not have been attributable to substrate disturbance alone, but in combination with light, as the effect was observed in treefall pits (Cook & Lyons 1983), characterized by both substrate disturbance and increased light.

7.3 Light

The complete lack of significant interaction, between treatment and light on biomass, flower, first year fruit production, and seed production suggests that substrate disturbance can lead to increased fecundity in the absence of increased light. Although light did not significantly interact with treatment in almost all cases and the amount of variability explained in the goldenseal responses due to light is quite low, the analyses nevertheless suggest that light has a positive influence as indicated by the correlation coefficients.

Pooling the goldenseal response over treatment plots could be used to remove a source of variation since each treatment has the same light measurement (recall one light measurement taken in the center of each block); however, pooling over treatment would cause a loss of information since the treatments vary with respect to the goldenseal response (i.e., biomass, flowers, fruit, seedlings, etc.). For example, some treatments produced more seeds than others under the same amount of light; thus, examination of the relationship between light and seed production, using the total number of seeds produced per block, would overestimate the relationship.

The slightly negative and minimal correlation between light and biomass, flower, and fruit production in the first year, compared to the positive correlations in the second year can be explained in several ways. For example: (1) light may not be an influence when environmental conditions are more favourable for growth (i.e., in 2000) because the plants can respond just as well in reduced light as in higher light; (2) trees may have produced much larger leaves during the wet and cool growing season of 2000; thus, much less light would have reached the forest floor and influenced growth; and/or (3) other environmental conditions could have reduced growth even in the presence of a greater amount of light. Overall, it may not have been valid to compare light measurements that were taken in the second year to production of biomass, flowers and fruit in the first year due to potential differences in the forest canopy including number of branches and twigs, leaf production, leaf size, and areas of leaf density. Thus, results based on second year data are more reliable.

The positive correlations, and stronger correlations compared to the other goldenseal responses, between light and both occurrence of germination and number of seedlings was expected since the most seedlings occurred at the site which was an open woodland edge and had the lowest amount of canopy cover.

8. Conclusions

Although direct increase in recruitment, in terms of germination, was not observed, disturbance simulation, involving substrate turnover alone and in combination with fertilization, clearly promotes growth and recruitment potential of goldenseal. Light contributed to, but was not essential for, the increase. Results support the observed association of goldenseal with disturbed areas of the woods (Section 3.3.3) and suggest that goldenseal may in fact be "waiting", or surviving between periods of population expansion (Section 3.1) that follow disturbance events accompanied by soil turnover and nutrient input.

9. Theoretical and Management Implications

The experimental results lend further support to a beneficial effect of substrate disturbance, which not only plays a role in increasing colonization of woodland herbs in treefall pits (Thompson 1980) and in canopy gaps (Hughes 1992), but may also promote their growth and increased reproductive output without a canopy opening. This finding is contrary to the perception based on numerous studies (Metzger & Schultz 1981; Davison & Forman 1982; Moore & Vankat 1986; Jenkins & Parker 1999) that canopy gaps alone increase recruitment potential.

In addition to canopy gaps, substrate disturbance is an important consideration in the understanding of woodland herb ecology. Results support the hypothesis that lack of specific kinds of disturbance, that no longer occur to the same degree as they did in the past, may contribute to causing rarity of certain woodland herbs. Thus, the assumption that undisturbed conditions are optimal for rare woodland plants may not be valid in the assessment of the conservation value of plant species, for example, in floristic quality indices. Management of mature woodlands involving disturbance simulation may be important, specifically for the protection of certain rare herbs.

Recovery of goldenseal from the "threatened" risk category can be achieved through transplanting into plots with substrate turnover alone or in combination with fertilization, with resultant increase in area of occurrence and area of occupancy. The results suggest that disturbance-simulation, involving transplanting with substrate turnover alone or with fertilization, within existing goldenseal habitat, increases the growth and reproductive output of goldenseal which may further contribute to population expansion. Since transplanting rhizomes is more reliable compared to sowing seeds, in terms of increasing the number of patches, rhizomes offer the most practical management tool. However, sowing seeds should also be used, especially in increased light, given the potential for genetically distinct individuals. Sowing seeds may be a more effective tool than demonstrated here since the seedling stage is very susceptible to environmental conditions and there were two extremes in conditions during the years of study. In a table of annual temperature and precipitation departures, ranked from warmest to coolest and wettest to driest, respectively, for the period 1948 to 2001 (54 years): 1999 was ranked second for temperature and 36th for precipitation; 2000 was ranked 15th for both temperature and precipitation; and 2001 was ranked 4th for temperature and 41st for precipitation (Climate Trends and Variations Bulletin for Canada 2001). Thus, both 1999 and 2001 were extraordinarily hot and dry whereas 2000 was comparatively very cool and wet. The cultivation literature warns that seeds "should never be allowed to dry out" (e.g., Davis 1996) and the seeds likely perished in the dry soil shortly after planting in mid-to-late July of 1999. Increased seed germination may be achieved when seeds are planted in a season with greater precipitation. Managers could employ transplanting both rhizomes and seeds with disturbance-simulation to assist in the recovery of goldenseal.

In terms of technology transfer, information regarding observations, survey, and experimental results has been provided to managers of goldenseal populations in Ontario in order to assist in protection and recovery. Site summaries, which provide information on population location and size, habitat size, soil, and other ecological features, are on file with the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the Ontario Natural Heritage Information Centre. Individual site summaries as well as instructions for population monitoring were sent to landowners with a conservation mandate, including Walpole Island Heritage Centre and conservation authorities. An update status report was provided to COSEWIC and assisted in the re-evaluation of goldenseal status. An article on cultivating goldenseal was published in a popular agricultural journal to promote protection, which was then duplicated on the United States Department of Agriculture Plants Database Website. A conservation network is in place as a result of bi-annual landowner contact through various media including phone calls, letters, pamphlets, and newsletters. As a result of this communication, several landowners are prepared and willing to serve on a recovery team once initiated. Technical reports on the goldenseal project were provided annually to World Wildlife Fund Canada and the Canadian Wildlife Service as part of the Endangered Species Recovery Fund requirements. These reports and several publications may assist in the development of a recovery team and a recovery plan.

Part III: Projection Matrix Analysis to Evaluate Need for Disturbance-Simulation Management

Projection matrix analysis was used to further evaluate the need for recovery actions and further assess whether goldenseal populations are "waiting", or surviving, for environmental conditions conducive to spread. While stem counts are useful as a method of demographic analysis and assisted in the assessment of limiting factors (Section 2.1.2), projection matrix analysis takes stem counts further and enables calculation of growth rates, identification of factors influencing growth rates, and proposition of underlying mechanisms (Gagnon 1999, Caswell 2001). The quadrats established in 1998 for examination of population trends based on stem counts (Section 2.1.2) were used to collect additional data in 2001 and all maps were re-evaluated. Stems were classified according to nine classes, taking seedlings and vegetative stems into account. Complete methods are described below.

10. Materials and Methods

10.1 Study Sites

The population dynamics of 14 populations were studied. Populations 1, 2, 3, and 4 were near the town of Arner (42° 02′ N, 82° 49′ W) and population 5 was near the town of Amhertsburg (42° 06′ N, 83° 06′ W) in Essex County. Populations 6, 7, and 8 were near the town of Wallaceburg (42° 36′ N, 82° 23′ W), population 9 was near the town of Duthill (42° 41′ N, 82° 23′ W), population 10 was near the town of Uttoxeter (43° 02′ N, 82° 03′ W), and population 11 was near the town of Watford (42° 57′ N, 81° 53′ W) in Lambton County. Population 12 was near the town of Bothwell (42° 38′ N, 81° 52′ W) in Kent County, population 13 was near the town of Arkona (43° 04′ N, 81° 50′ W) in Lambton County, and population 14 was near the town of Goderich (43° 45′ N, 81° 43′ W) in Huron County. Site numbers that coordinate with a file maintained by the Chairman of the Subcommittee for Plants, Committee on the Status of Endangered Wildlife in Canada (COSEWIC) are provided rather than exact locations for conservation reasons.

10.2 Field Methods

In May of 1998, a 1m^2 quadrat was placed towards the edge of a single patch (i.e., not in dense centre or sparse edge) within each of the 14 populations. There was no evidence of harvest or recent disturbance at any of the populations. Each quadrat was permanently marked with four aluminum pins and a numbered aluminum tag. Some populations had more than one patch and patch size varied in terms of ramet number. Thus, in some cases the sample is more representative of the entire population than in others. Representation of a quadrat sample ranged from 2.4 to 98.1% of the total number of stems in the patch with a mean of 35.1% and from 1.5 to 71.1% of the total number of stems in a population with a mean of 21.6%. Quadrats were visited in May and July for three years (1998, 2000, 2001), except for the quadrat in population 2 which had been moved in 2001. All ramets were mapped within each quadrat according to the following size classes which were selected based on reproductive state: small (immature stem with single leaf ≤12.5 cm in width); large (mature stem with single leaf > 12.5 cm in width); and flowering (mature flowering stem with two or more leaves). Presence or absence of seedlings was noted. Fruiting ramets were recorded in July and pericarp divisions were counted as an estimate of seed production in 2001. The flowering ramets are produced by larger rhizomes which are presumed to be the oldest. The smallest ramets are generally associated with the rhizomes or root tips of larger ramets. Daughter ramets were identified as those immediately adjacent to the stem of another ramet. Ramet connections and age were not confirmed due to: (1) likely damage to rhizomes, rootlets, and/or buds by digging as they are often tightly intertwined and knotted with others; (2) parts of the rhizome may have decomposed; (3) ramets that develop from root tips eventually lose their connection to the original rhizome; and (4) goldenseal, like most plants, has size-dependent sexual reproduction, and thus as a general rule, size is considered a better state variable than age for demographic analyses of plants (Caswell 2001).

10.3 Data Analysis

The projection matrix model (Caswell 2001) summarizes the fate of individuals in the population from year one to year two in terms of survival, growth, and reproduction. It is considered a powerful tool (Nault & Gagnon 1993) and a standard method (Silvertown *et al.* 1996) for analysing population dynamics of plants. It has been used by several authors for plants such as the endangered ginseng (*Panax quinquefolius* L., Charron & Gagnon 1991), vulnerable northern populations of wild leek (*Allium tricoccum* Ait., Nault & Gagnon 1993), the endangered Furbish's lousewort (*Pedicularis furbishiae* S. Wats., Menges 1990), and common herbs including wild ginger (*Asarum canadense* L., Damman & Cain 1998), and jack-in-the-pulpit (*Arisaema triphyllum* L., Bierzychudek 1982). The model has the following form: $n_{t-1} = \mathbf{A}n_t$, where n_t is a column vector corresponding to the structure at time t of a population classified into s classes, and $\mathbf{A}$ is the matrix of transitions of order s. Each cell in the matrix represents the probability of transitions between classes in a year. After several iterations, the population converges to a stable size distribution (**w**) characterized by a fixed reproductive value distribution (**v**) and a constant growth rate (λ). Population growth trends are based on λ values. When $\lambda > 1.0$ the population is increasing, $\lambda = 0$ the population is at equilibrium or stable, and when $\lambda < 1.0$, the population is decreasing (Caswell 2001, Nault & Gagnon 1993, Gagnon 1999).

The size classes (*s*) used were: *l* = ramet with one leaf ≤12.5 cm in width; L = ramet with one leaf >12.5 cm in width; F = flowering ramet with two or more leaves. A seed class was added to account for seedlings that germinated within the time period. In order to distinguish between production of daughter ramets and size decrease, three additional classes were used in the transition matrix for daughter or vegetative (V) ramets: V*l*, VL, and VF. The life cycle diagram for goldenseal is as follows:

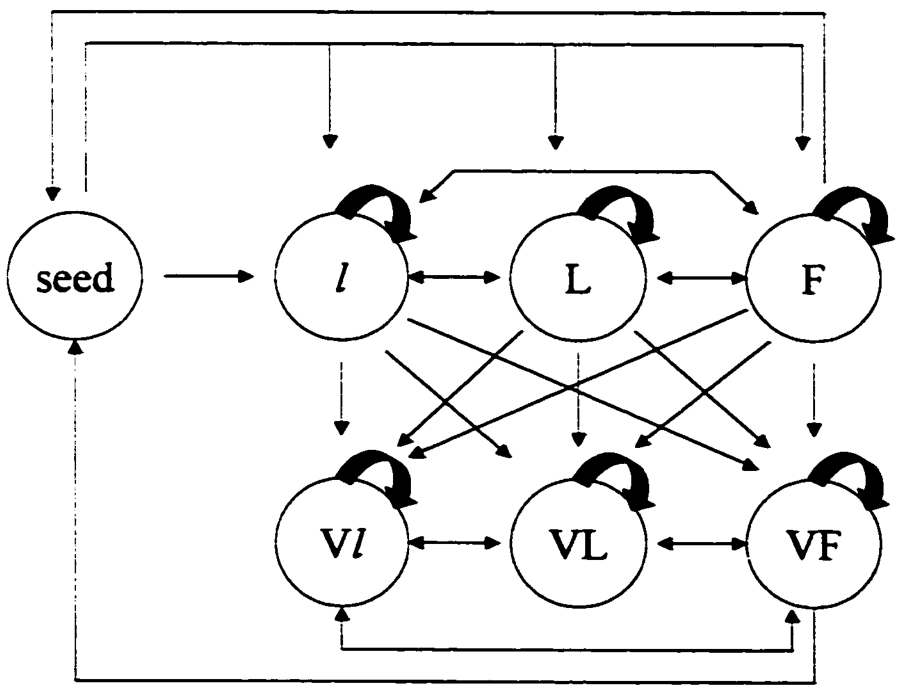

Figure 13. Life cycle diagram for goldenseal. *l* = ramet with one leaf ≤12.5 cm in width; L = ramet with one leaf >12.5 cm in width; F = flowering ramet with two or more leaves. V = vegetative ramet.

The first row of the matrix contains the annual mean seed production per ramet of the corresponding class (recall only size class F ramets produce seed). If a rhizome produced more than one ramet of the same class in the following year, its transition probability was multiplied by the number of ramets. For example, two size class *l* ramets exist in year one. One of the ramets produces three size class V*l* ramets in year two, giving a transition probability for size class *l* to size class V*l* of 1.5 (i.e., 1/2 x 3) since the ramet made the same transition three times. This transition probability is exactly the same contribution as if three small ramets produced a small ramet each. Thus, in some cases cells may have a transition probability greater than one. Seed production for the 1998 to 2000 matrices was estimated as 15 seeds per size class F ramet. This was based on the average number of seeds within 40 ripe fruits randomly selected from goldenseal patches at four different sites. Seed production for the 2000 to 2001 matrices was estimated based on fruit produced in 2001 because 2000 data were unavailable. The number of pericarp divisions per fruit were counted so as to avoid squashing fruit and interfering with seed dispersal. Several berries were squashed to confirm that the number of pericarp divisions equalled the number of seeds, however this method may slightly overestimate seed production as it does not account for seeds not fully developed. The total number of pericarp divisions produced in 2001 by 2000 ramets was divided by the total number of size class F ramets in 2000 to obtain the average seed production for 2000. If the ramet produced fruit in 2000 but not in 2001, its seed production was estimated as the average number of pericarp divisions per ramet in 2001 (total number of pericarp divisions divided by total number of fruiting ramets). This method was applied to all sites except for site 12, which lacked enough berries to obtain an average. In this case, seed production was estimated as 15 seeds per ramet as in 1998 above. It was assumed that there were approximately the same number of seeds produced in 2000 as in 2001 since fruits of goldenseal do not vary in size to a great degree from year to year unless ramet size has varied. For each population, seedling recruitment rates (seed to size class *l*, L, or F) were estimated by dividing the number of seedlings in year two by the number of seeds produced in year one. This may provide an over-estimate of recruitment for each sample given that seedlings in each quadrat could have arisen from seed produced outside of the quadrat. Fourteen matrices were produced (one for each population) for 1998 to 2000 as well as an overall matrix of transitions based on ramets from all samples combined. Data for one of the populations were unavailable in 2001; therefore 13 separate matrices were produced for 2000 to 2001 as well as an overall matrix. Elasticity matrices were then computed to examine the matrix elements most important to population growth. Elasticity values represent the relative contribution of the matrix elements to the population growth rate (λ, Caswell 2001).

There was considerable annual variability in matrix values within and among populations (Appendix C, Table 1); therefore, Monte-Carlo simulation analysis was used to generate a probability distribution for dominant eigenvalues (growth rates) to assist in evaluation of error in the estimation of the growth rates. Random variables for transition values were generated using a beta distribution function with parameters determined by the mean transition value and standard deviation (0.4 +/- 0.3 for both 1998-2000 and 2000-2001, Appendix C, Table 1). Transition values for seed to small, large, or flowering ramets were much lower than those for other transitions, and therefore, random variables were generated in the seed column using a beta distribution function with the mean seed transition value and standard deviation (0.06 +/- 0.04 for 1998-2000 and 0.07 +/- 0.08 for 2000-2001, Appendix C, Table 1). The beta distribution was chosen because the generated random variables vary between 0 and 1. A poisson distribution function was used to generate random variables for seed production values since the distribution takes on the values 0, 1, 2, 3, etc., and is often used as a model for the number of events or occurrences in a specific time period. The function used mean seed production over all matrices (9.06 for 1998-2000 and 8.84 for 2000-2001). Only those cells in the matrix that had transition values greater than zero were randomized. It is assumed that all possible transitions were accounted for by randomizing each of the matrices and then using the corresponding growth rates in the Monte-Carlo analysis. Each matrix was re-calculated 100 times in Monte-Carlo analysis and all resulting growth rates were presented in a single histogram representing the probability distribution for growth rates in goldenseal. Results were combined into one histogram since the two sets of matrices had either the same mean and standard deviation for transition values or the difference between means was not statistically significant.

11. Results and Discussion

11.1 Projection Matrix Analysis

The projection matrix analysis supports the survey and stem count observations that goldenseal populations are not spreading. The 27 transition matrices (Table 1 in Appendix C) summarize trends between consecutive years. Although transition probabilities varied with size class and year, examination of the dominant transitions, within and across size classes, reveals little change in population structure. Ramets tended to remain in the same size class, as 16 out of the 26 matrices with size class *l* ramets (62%), 19 out of the 27 matrices with size class L ramets (70%), 20 of the 26 matrices with size class F ramets (77%), and 16 of the 21 matrices with size class V*l* (76%) had dominant transitions to the same class. VL and VF ramets either decreased by one size class or remained in the same class. The overall matrices (all samples combined) also demonstrate little change in population structure. The dominant transition within each size class was to the same size class, with the exception of VL ramets from 1998 to 2000 which decreased to size class V*l*. Thus, there is relatively little change in population structure as goldenseal ramets simply maintain their current size.

Examination of the transitions to and between vegetative classes reveals the importance of vegetative propagation for population growth. In terms of transitions to vegetative classes, the ramets in size class *l*, L, and F produced the most (or only) ramets in size class V*l*. F class ramets also produced VL ramets in some cases. Out of 24 matrices where V*l* ramets were produced, the dominant transition was from size class F in 10 cases, size class L in nine cases, and from size class *l* in five cases. Out of 13 matrices where VL ramets were produced, the dominant transition was from size class F in 6 cases, size class L in five cases, and from size class *l* in two cases. Out of the three matrices where VF ramets were produced, the dominant transition was from size class L in two cases and size class *l* in the other. Size class F dominated the transition to V*l*, VL, and VF ramets in both the 1998 to 2000 and 2000 to 2001 overall matrices (with the exception of L to VF in the 2000-2001 overall matrix). Sums of transitions were often greater than 1.0 for the *l* (14 matrices), L (18 matrices), and F (16 matrices) size classes. Overall, sums were greater than 1.0 for the L and F classes from 1998 to 2000 and for the *l*, L, and F classes from 2000 to 2001. This indicates the importance of vegetative propagation. Vegetative propagation is critical in goldenseal populations, and in particular, the production and survival of small stems by large, flowering, and vegetative ramets.

The above trend in population structure and the importance of vegetative reproduction are demonstrated in Figures 14 through 16. Little change in population structure is evident upon examination of Figure 14 as the shape of the graph varies relatively little among years with losses of stems not corresponding to subsequent increases in other size classes. Figure 14 also demonstrates the importance of vegetative propagation with minimal or no production of seedlings and the only notable increase in stems occurring in the small vegetative size class in 2000. The prominent pathway for population growth by production of small vegetative offspring is also shown in Figures 15 and 16. Thirteen of the fourteen populations show an increase in small vegetative stems between 1998 and 2000 and the loss from the other population was minimal (i.e., one stem, Figure 15Ai). Increases are often greater in the small vegetative size class (Figure 15Ai) compared to the large (Figure 15Bi) and flowering (Figure 15Ai). Conversely, the majority of populations experienced losses in small and large stems in both sets of years (Figure 15Aiii and 15Biii) and either had no overall change (9 populations) or a decrease in flowering stems (2 populations, Figure 16Aiii). Gains in seedlings are much reduced compared to vegetative offspring, with only about half of the populations producing a few seedlings and usually only in one set of years. Seed production increased however, as approximately half of the populations showed a gain in fruit production even though there was no overall gain or a decrease in the number of flowering stems (Figures 14, 16Aiii and 16Biii). The increased number of fruiting stems is therefore a result of a greater proportion of flowering stems producing fruit, which may have been a consequence of the weather. No increase in seed production capability actually occurred. Seedling development is limited and growth of goldenseal populations is dependent on vegetative propagation. Therefore survival of vegetative offspring, as well as the large and flowering stems that primarily produce them, is critical to population growth.

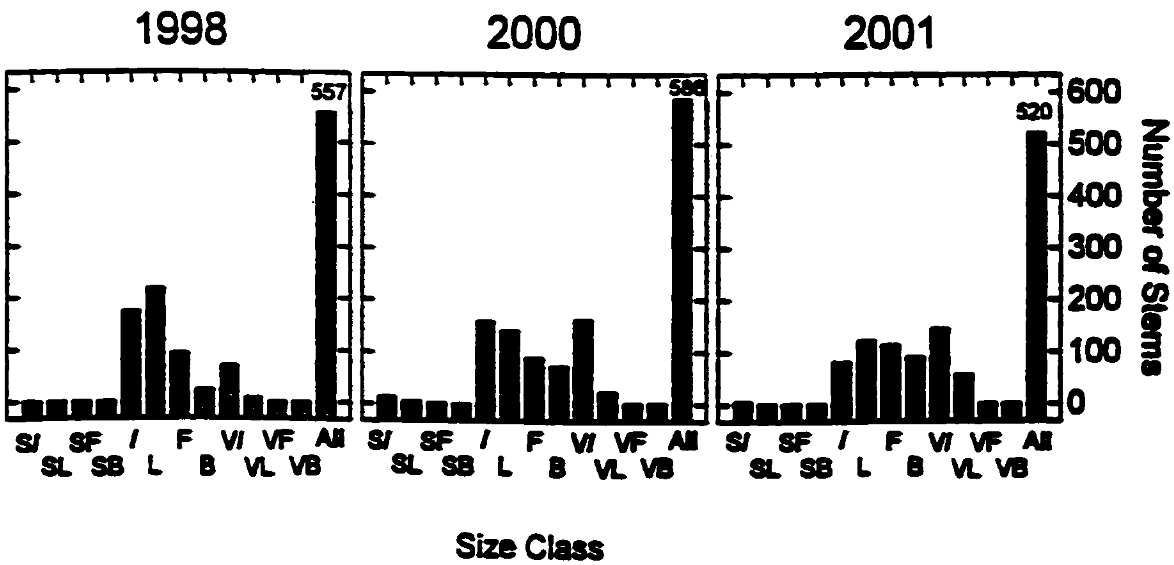

Figure 14. Overall trend in population structure, from 1998 to 2001, based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. *l* = ramet with one leaf ≤ 12.5 cm in width; L = ramet with one leaf > 12.5 cm in width; F = flowering ramet with two or more leaves, All = all ramets. S denotes stem developed from seed. V denotes stem developed from vegetative propagation.

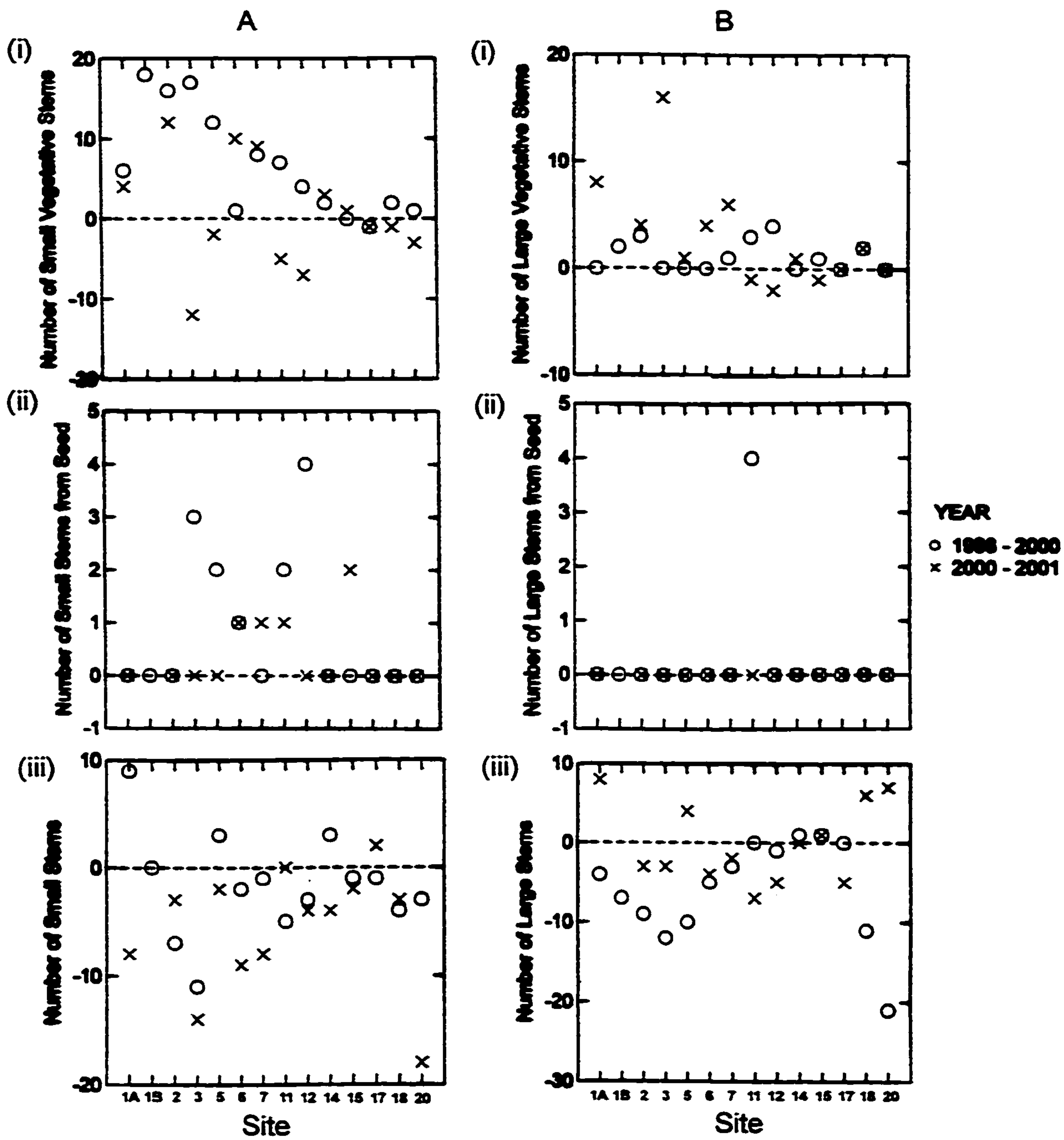

Figure 15. Increases or decreases in number of (A) small stems and (B) large stems, either (i) vegetative offspring, (ii) new stem from seed, or (iii) original stem, from 1998 to 2000 (O) and 2000 to 2001 (X), based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. Site numbers correspond to the locations file maintained by COSEWIC. Data were unavailable for Site 1B 2000 to 2001.

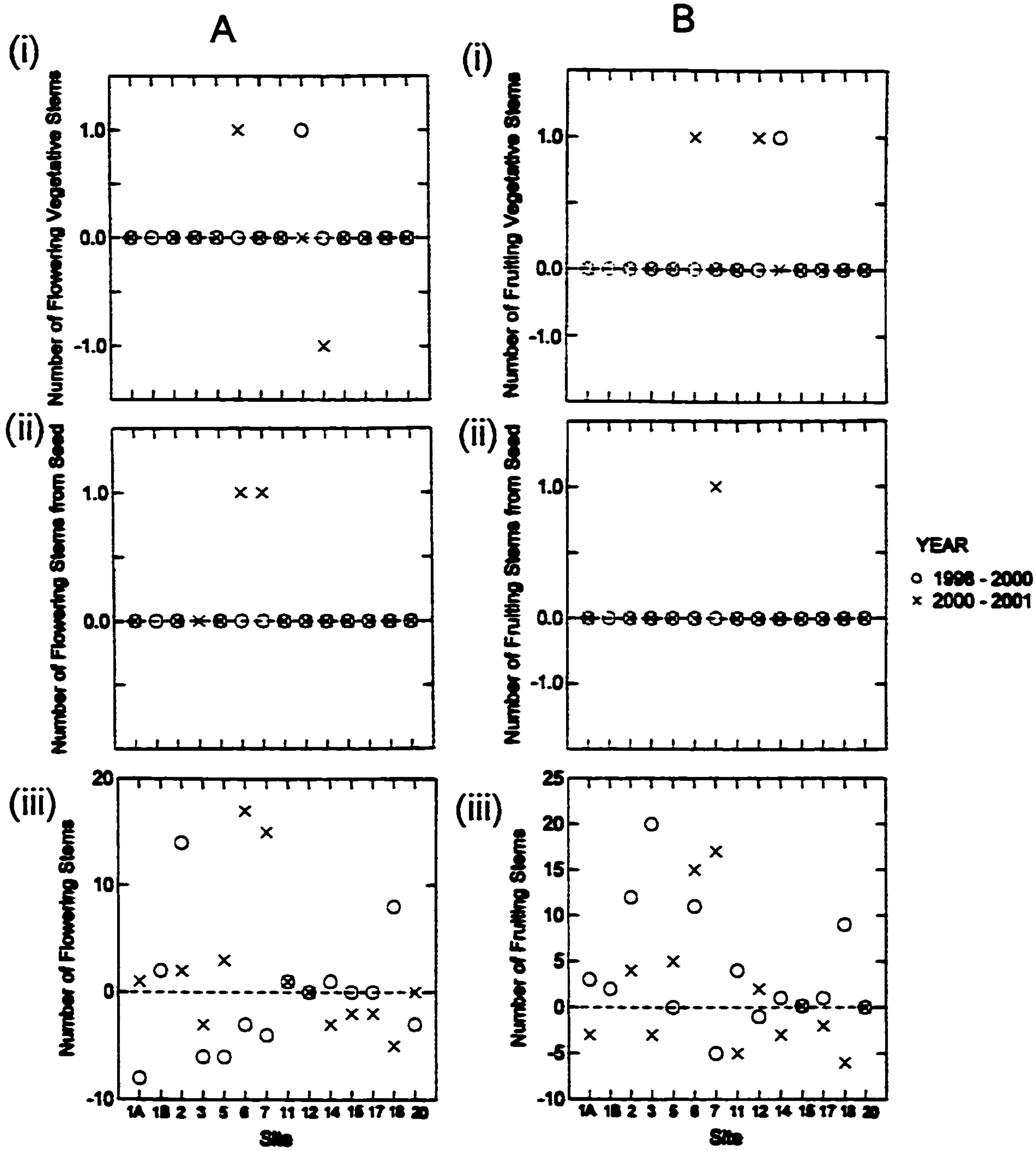

Figure 16. Increases or decreases in number of (A) flowering stems and (B) fruiting stems, either (i) vegetative offspring, (ii) new stem from seed, or (iii) original stem, from 1998 to 2000 (O) and 2000 to 2001 (X), based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. Site numbers correspond to the locations file maintained by COSEWIC. Data were unavailable for Site 1B 2000 to 2001.

Survival did not seem to be related to size class. Each size class had a high frequency of high mortality (> 30%), depending on the year, and approximately the same number of high mortality cases occurred between 1998 - 2000 and 2000 - 2001. High mortality more frequently occurred in vegetative classes and seed mortality was very high (> 85%) in all populations in both of the transition years (Table 7). Thus, vegetative offspring are more vulnerable than mother ramets and seeds usually do not develop, further indicating the dependence on survival of established ramets and vegetative propagation for population growth.

Table 7. Percentage mortality of goldenseal in the following size classes: s = seed, *l* = ramet with single leaf ≤ 12.5 cm width, L = ramet with single leaf > 12.5 cm width, F = flowering ramet with two or more leaves, V = vegetative or daughter ramet, for fourteen populations (Pop.) between 1998 - 2000 and 2000 - 2001. Population numbers correspond to the locations file maintained by COSEWIC.

	% Mortality													
	1998 - 2000							2000 - 2001						
	Class							Class						
Pop.	s	*l*	L	F	V*l*	VL	VF	s	*l*	L	F	V*l*	VL	VF
1A	0	0	20.0	16.7	0	0	0	0	0	0	0	0	0	0
1B	0	0	19.3	0	0	0	0				-			
2	0	17.6	4.1	0	50.0	0	0	0	20.0	6.7	6.2	45.8	0	0
3	0	65.3	42.9	22.6	0	0	0	0	46.7	50.0	20.0	16.7	0	0
5	86.7	16.7	25.0	44.4	33.3	0	0	0	0	0	0	46.7	0	0
6	93.3	41.2	7.6	33.4	0	0	0	96.0	0	25.0	0	0	0	0
7	0	33.4	13.0	33.3	18.2	0	0	86.0	0	0	50.0	5.2	45.0	0
11	93.4	12.5	10.0	33.3	66.7	0	0	98.0	40.0	35.7	0	80.0	33.4	0
12	94.7	66.7	18.2	14.3	55.6	0	0	0	66.7	40.0	66.7	69.2	75.0	0
14	0	50.0	0	0	0	0	0	93.0	0	0	50.0	0	0	0
15	0	0	0	0	0	0	0	75.0	0	50.0	0	0	0	0
17	0	0	12.5	0	50.0	0	0	0	0	50.0	0	0	0	0
18	0	36.4	10.5	0	40.0	0	0	0	14.3	12.5	7.6	0	0	0
20	0	25.6	42.9	33.3	50.0	0	0	0	17.5	28.6	0	54.5	0	0

The rate of population growth (λ) computed from transition matrices for 1988 - 2000 and 2000 - 2001 for the 14 populations varied between years and populations (Table 8). Three of the populations were at equilibrium ($\lambda = 1.0$) each year. Depending on the year, four of the populations were either stable or decreasing ($\lambda < 1$) and three were either stable or increasing ($\lambda > 1$). Two of the populations were decreasing in both years. One population was increasing in both years and another was decreasing in one year and increasing in the next. The fact that the computed growth rates (Table 8) do not correspond exactly to the increases or decreases in population size based on stem counts (Figure 17) demonstrates the importance of both methods in analysis of population trends. A population may have increased in stem number but depending on mortality rates, maturity rates, and rates of other demographic parameters such as seed production and recruitment, the increase in stems may not contribute to an increasing growth rate. Nevertheless, an increase in stem number is indicative of potential for population maintenance or an increased rate of growth. Both stem counts (Figure 14) and computed growth rates (Table 8) indicate little or no increase in goldenseal populations.

Table 8. Individual and mean growth rates (λ) (+/- standard deviation) from 1998 - 2000 and 2000 - 2001 for 14 goldenseal populations. Growth rates were calculated from transition probability matrices included in Appendix C. The overall matrix growth rates were calculated from transition probabilities based on ramets from all quadrat samples combined. Growth rates in parentheses are the corresponding annual rates. Matrices were not produced for 1998 - 1999 and 1999 - 2000 since data for 1999 were unavailable. Population numbers correspond to the locations file maintained by COSEWIC.

	Growth Rate (λ)	
	Transition	
Population	1998 - 2000	2000 - 2001
1A	1.000(1.000)	1.000
1B	1.000(1.000)	-
2	1.000(1.000)	0.930
3	1.000(1.000)	0.800
5	0.816(0.908)	1.000
6	1.000(1.000)	1.248
7	0.793(0.897)	1.308
11	1.061(1.030)	1.012
12	0.952(0.974)	1.000
14	1.000(1.000)	1.210
15	1.000(1.000)	1.000
17	0.917(0.958)	0.667
18	1.119(1.060)	1.000
20	0.721(0.861)	0.754
Mean	0.956 +/- 0.109	0.995 +/- 0.186
	0.986 +/- 0.133	
Overall Matrix	0.889(0.945)	0.927

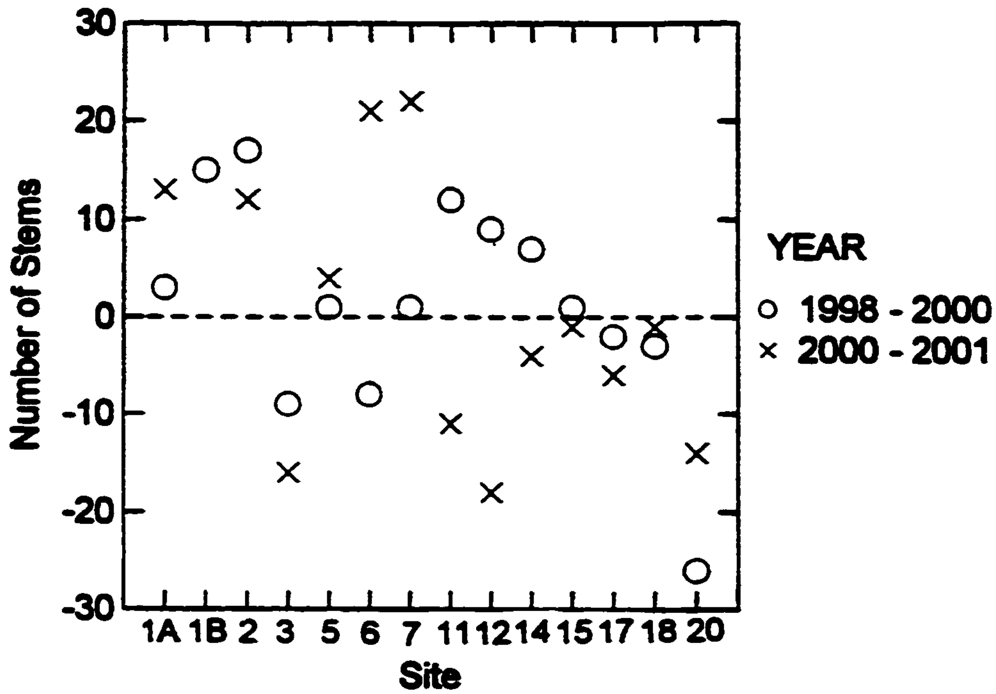

Figure 17. Increases or decreases in total number of stems, from 1998 to 2000 (O) and 2000 to 2001 (X), based on a 1 m^2 quadrat sample from each of 14 goldenseal populations in Ontario. Site numbers correspond to the locations file maintained by COSEWIC. Data were unavailable for Site 1B 2000 to 2001.

The overall rate of decline can be examined in several ways. The mean growth rate for the 1998 to 2000 transition (0.956) suggests that goldenseal is declining at a rate of 4.4% every two years (+/- 10.9%). The growth rate computed from the overall matrix (0.889) suggests decline at a rate of 11.1% every two years . The mean growth rate for the 2000 to 2001 transition (0.995) suggests that goldenseal is declining at a rate of 0.5% per year (+/- 18.6%) and the growth rate computed from the overall matrix (0.927) suggests decline at a rate of 7.3% per year. The mean growth rate for both transitions (0.986, two year transition rates were converted to annual rates), suggests that goldenseal is declining at a rate of 1.4% per year (+/- 13.3%). The Monte-Carlo simulation analysis suggests that the actual growth rate is slightly higher at 1.04 +/- 0.35. Thus, the various calculated growth rates indicate that goldenseal is slightly increasing to slightly declining in growth, or in other words, nearly stable.

The Monte-Carlo analysis also provides an estimate for the probability of extinction. According to the probability distribution of growth rates for goldenseal (Figure 18), there is a approximately a 50:50 chance of extinction overall (i.e., 1340 out of 2700 counts below growth rate of 0.99) and extinction in the near future is unlikely. For example, based on the total number of stems estimated for Ontario (14 665 stems, see Table 4, Section 3.3.3) there is a 0.2% chance of extinction within five years, a 1.3% chance of extinction within 8 years, a 6.3% chance of extinction within 16 years, a 15.4% chance of extinction within 29 years, a 23.3% chance of extinction within 44 years, a 35.6% chance of extinction within 83 years, and a 50% chance of extinction within 479 years. These probabilities however do not take into account environmental variation and therefore likely underestimate the actual probability of extinction for goldenseal in Ontario.

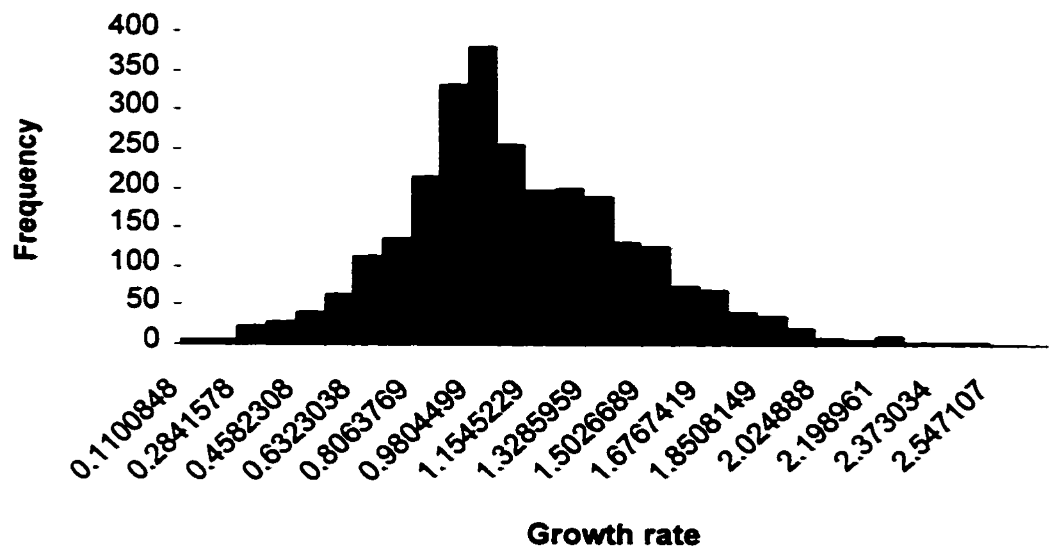

Figure 18. Frequency of growth rates generated by Monte-Carlo analysis. Growth rates were re-calculated 100 times for each of 27 randomized matrices. Each matrix represented a 1 m^2 quadrat sample from a single population of goldenseal in southwestern Ontario. Labels on the x-axis are upper growth rates.

A slow growth rate is expected of a perennial herb in a relatively stable woodland environment (Gagnon 1999). Goldenseal is similar to other woodland perennials, such as American ginseng (*Panax quinquefolius* L.) with a population growth rate varying between 0.88 and 1.17 (Charron & Gagnon 1991), fairy wand (*Chamaelirium luteum* (L.) A. Gray) with a growth rate varying between 0.99 and 1.06 (Meagher 1982), jack-in-the-pulpit (*Arisaema triphyllum* L.) with a growth rate varying between 0.85 and 1.32 (Bierzychudek 1982), wild leek (*Allium tricoccum* Ait.) with a growth rate varying between 1.02 and 1.13 (Nault & Gagnon 1993), and wild ginger (*Asarum canadense* L.) with a growth rate varying between 0.77 and 1.108 (Damman & Cain 1998). Conversely, in disturbed habitats, where more resources such as light and nutrients are made available, plants tend to have highly variable population growth rates such as 0.58 to 1.81 in Furbish's lousewort (*Pedicularis furbishae* S. Wats., Menges 1990), 0.28 to 2.61 in teasel (*Dipsacus sylvestris* Hudson, Werner & Caswell 1977), 0.77 to 1.65 in sheathed cotton-grass (*Eriophorum vaginatum* L., Fetcher & Shaver 1983), and 0.60 to 1.43 in downy oatgrass (*Danthonia sericea* Nutt., Moloney 1988).

11.2 Elasticity Matrix Analysis

The 27 elasticity matrices and reproductive values (eigenvector **v**) summarize the importance of size classes to the growth rate (Table 2 in Appendix C). Each elasticity matrix was constructed by transforming each cell in the transition matrix in order to express its specific contribution to the growth rate (Caswell 2001). The cells with the largest values in the elasticity matrix indicate which transition, or transitions, contribute the most to the growth rate (Gagnon 1999). The highest elasticity value was obtained most often by the F to F transition, with an average contribution to the growth rate of 75.3%, followed by the V*l* to V*l* transition, with an average contribution of 86.9%, the L to L transition, with an average contribution of 66.8%, the *l* to *l* transition, with an average contribution of 74.5%, the VL to VL transition, with an average contribution of 92.2%, the V*l* to VL transition, with an average contribution of 39.3%, and finally, the VL to VF transition, with a contribution of 100% (Table 9). The F to F transition obtained the highest elasticity value in both overall matrices with contributions of 21.6% (1998 to 2000) and 60.2% (2000 to 2001). The reproductive value (eigenvector **v**) is a measure of the value of an individual as a seed for future population growth which takes into account the amount of future reproduction, the probability of surviving to realize reproduction, and time required for production of offspring (Caswell 2001). Values were highest for size class F, in just over half of the matrices and in both overall matrices, and decreased with decreasing size of the ramet (Table 9). For the remaining individual matrices, the highest reproductive values varied by size class. Thus, the classes having the strongest influence on the growth rate varied with population and year, and flowering ramets and vegetative propagation were the most valuable in terms of reproduction.

Table 9. Highest elasticity values and reproductive values (v) from transition matrices for 14 goldenseal populations between 1998-2000 and 2000-2001.

Pop.	Year	Transition	Elasticity Value	Size Class	v
1A	1998 - 2000	*l* - *l*	1.000	*l*	0.400
	2000 - 2001	-	-	*l*, L, F	0.333
1B	1998 - 2000	V*l* - V*l*	1.000	F	0.362
2	1998 - 2000	F - F	1.000	F	0.394
	2000 - 2001	V*l* - VL	0.285	F	0.400
3	1998 - 2000	V*l* - V*l*	1.000	F	0.396
	2000 - 2001	F - F	0.800	F	0.846
5	1998 - 2000	*l* - *l*	0.639	F	1.000
	2000 - 2001	*l* - *l*	0.595	*l*	0.585
6	1998 - 2000	V*l* - V*l*	1.000	V*l*	0.749
	2000 - 2001	F - F	0.595	F	0.394
7	1998 - 2000	V*l* - V*l*	0.904	L	0.404
	2000 - 2001	V*l* - V*l*	0.485	*l*	0.354
11	1998 - 2000	F - F	0.280	F	0.444
	2000 - 2001	F - F	0.968	F	0.892
12	1998 - 2000	L - L	0.232	F	0.523
	2000 - 2001	VL - VL or VF	1.000	-	0
14	1998 - 2000	L - L	1.000	-	0
	2000 - 2001	V*l* - V*l*	0.827	L	0.290
15	1998 - 2000	-	-	F, VL	0.500
	2000 - 2001	L - L, F - F	1.000	F	1.000
17	1998 - 2000	V*l* - VL	0.500	VL	0.467
	2000 - 2001	F - F	0.667	VL	0.706
18	1998 - 2000	VL - VL	0.767	F	0.500
	2000 - 2001	VL - VL	1.000	V*l*, VL	0.456
20	1998 - 2000	-	-	F	1.000
	2000 - 2001	L - L	0.440	*l*	0.561
Overall	1998-2000	F - F	0.216	F	0.536
	2000-2001	F - F	0.602	F	0.470

The major elasticity values for each matrix show that survivorship of large ramets, large flowering ramets, and their small vegetative offspring, has the strongest influence on the population growth rate. These ramets contribute much more to the growth rate if they remain in the same size class in the next year rather than grow to the next class (or in the case of large flowering stems, decrease in size). Similarly, the stability of American ginseng (*Panax quinquefolius* L.) populations is more sensitive to a decrease in the survival rate of large individuals than to a reduction in the production of seeds or in the establishment of seedlings (Charron & Gagnon 1991), and the growth rate of wild ginger (*Asarum canadense* L.) populations is most strongly affected by survivorship of established plants (Damman & Cain 1998). Wild leek (*Allium tricoccum* Ait.) also has a survival strategy characterized by maintenance of a large ramet size that can flower and then divide to supply additional middle-sized ramets to the population (Nault & Gagnon 1993).

12. Conclusion

The projection and elasticity matrix analyses indicate, based on the years of observation in the absence of both disturbance and harvest, that goldenseal is a slow-growing perennial herb. Contrary to plants in disturbed habitats that can have growth rates well above equilibrium, growth in goldenseal populations is near equilibrium and dependent on high rates of survival of established plants and vegetative propagation. This further suggests that environmental conditions required for population increase are lacking and further supports the survey and stem count observations that Ontario goldenseal populations have remained stable over decades and expanded slowly (Sections 3.1.1 and 3.1.2). Evidence of harvesting was not found at any of the populations; therefore, the lack of population increase is not considered a result of harvesting and investigation of the impacts of harvest by manipulating the transition matrices was not carried out. Although the projection matrix analysis can not predict future trends, since environmental conditions change from year to year, the analysis supports observations concerning goldenseal status based on survey and stem count results. Populations are not spreading.

Results of the projection matrix analysis, in addition to the population survey and comparison of stem counts, represent extensive evidence indicating that action must be taken to recover goldenseal from the threatened category. Results of the field experiment and projection matrix analysis together suggest that in the absence, or reduced frequency and severity, of substrate and canopy disturbance similar to that caused by major disturbance events in the past such as flooding, fire, and effects of extinct and extirpated birds and mammals, goldenseal simply persists but does not increase. Populations appear to be awaiting disturbance events of a type that are no longer present or frequent on the landscape. The projection matrix analysis and experimental results emphasize the need and importance to proceed with disturbance simulation in order to recover goldenseal from the threatened category.

13. References

Abdel-Haq, H., M. F. Cometa, M. Palmery, M. G. Leone, B. Silvestrini, and L. Saso. 2000. Relaxant effects of *Hydrastis canadensis* L. and its major alkaloids on guinea pig isolated trachea. Pharmacology and Toxicology 87(5):218-222.

Abourashed, E. A., and I. A. Khan. 2001. High performance liquid chromatography determination of hydrastine and berberine in dietary supplements containing goldenseal. Journal of Pharmaceutical Sciences 90(7):817-822.

Aguilera, M. O., and W. K. Lauenroth. 1995. Influence of gap disturbance and type of microsites on seedling establishment in *Bouteloua gracilis*. Journal of Ecology 83:87-97.

Akhter, M. H., M. Sabir, and N. K. Bhide. 1977. Anti-inflammatory effect of berberine in rats injected locally with cholera toxin. Indian Journal of Medical Research 65:133-141.

Allen, G. M., Eagles, P. F. J. & S. D. Price (eds). 1990. Conserving Carolinian Canada. University of Waterloo Press, Waterloo, Ontario.

Amin AH, T. V. Subbaiah, and K. M. Abbasi. 1969. Berberine sulfate: antimicrobial activity, bioassay, and mode of action. Canadian Journal of Microbiology 15:1067-1076.

Arno, S. F. 1996. The seminal importance of fire in ecosystem management - impetus for this publication. Pages 3-5 *in* The use of fire in forest restoration. USDA General Technical Report INT-GTR-341.

Babbar, O.P., V. K. Chhatwal, I. B. Ray, and M. K. Mehra.1982. Effect of berberine chloride eye drops on clinically positive trachoma patients. Indian Journal of Medical Research 76(Suppl):83-88.

Barton, B. S. 1978 & 1804. Collections for an essay towards a materia medica of the United States. Reprint ed. 1900. Bulletin of the Lloyd Library, No. 1, Reproduction Series, No. 1.

Beattie, A. J. 1971. Pollination mechanisms in *Viola*. New Phytologist 70:343-360.

Bertin, R. I., and O. D. V. Sholes. 1993. Weather, pollination and the phenology of *Geranium maculatum*. American Midland Naturalist 129:52-66.

Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs 52:335-351.

Bormann, F. H., and G. E. Likens. 1979. Catastrophic disturbance and the steady state in northern hardwood forests. American Scientist 67:660-669.

Bowles, H. 1891. A contribution to the life history of *Hydrastis canadensis*. Botanical Gazette 16:73-82.

Brewer, R. 1980. A half-century of changes in the herb layer of a climax deciduous forest in Michigan. Journal of Ecology 68:823-832.

Budzinski, J. W., B. C. Foster, S. Vandenhoek, and J. T. Arnason. 2000. An in vitro evaluation of human cytochrome P450 3A4 inhibition by selected commercial herbal extracts and tinctures. Phytomedicine 7(4):273-282.

Burke, D. M., and E. Nol. 1998. Edge and fragment size effects on the vegetation of deciduous forests in Ontario, Canada. Natural Areas Journal 18(1):45-53.

Canadian Wildlife Service. 1999. CITES Information Notes. Environment Canada. 3 pages. Web site http://www.cws-scf.ec.gc.ca/cites/note1_e.html. Accessed 01/02.

Carson, W. P., and S. T. A. Pickett. 1990. Role of resources and disturbance in the organization of an old-field plant community. Ecology 71:226-238.

Caswell, H. 2001. Matrix Population Models, 2nd Ed. Sinauer Associates, Inc. Sunderland, Massachusetts.

Catling, P. M.. 2001a. Protecting vascular plant biodiversity in Canada: progress and problems with the taxon approach. Pages 62-81 *in* Bioconservation and Systematics: Proceedings of the Canadian Botanical Association Conference Symposium in London, Ontario, June 2000 (eds J. B. Phipps and P. M. Catling). Canadian Botanical Association.

Catling, P. M. 2001b. Extinction and the importance of history and dependence in conservation. Biodiversity 2:2-14.

Catling, P. M., and J. Cayouette. 1996. Vascular Plant Biodiversity in the Mixedwood Plains Ecozone *in* Assessment of species diversity in the Mixed Plains ecozone. Agriculture Canada, Biological Resources Division. Central Experimental Farm, Ottawa. Web site http://www.cciw.ca/eman-temp/reports/publications/Mixedwood/plants/intro.html. Accessed 01/02.

Catling, P. M., and A. Sinclair. 2000. A basis for the use of fire in protection and management of biodiversity in the alvar landscape of the Burnt Lands, Regional Municipality of Ottawa-Carleton, Ontario. Ontario Ministry of Natural Resources. 14 pages.

Centre Europ,en d' tudes des Polyphosphates. 2002. Phosphate Recovery. Web site http://www.nhm.ac.uk/mineralogy/phos/ Accessed 04/02.

Channell, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84-86.

Chapman, J. A., and G. A. Feldhamer (eds). 1982. Wild mammals of North America. The Johns Hopkins University Press, Baltimore. 1147 pages.

Charron, D., and D. Gagnon. 1991. The demography of northern populations of *Panax quinquefolius*(American Ginseng). Journal of Ecology 79:431-445.

CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). 2000. CITES-listed Species Database: Flora. Web site http://www.cites.org. Accessed 01/02.

Ckless K, Schlottfeldt JL, Pasqual M, *et al.* 1995. Inhibition of in-vitro lymphocyte transformation by the isoquinoline alkaloid berberine. Journal of Pharmacy and Pharmacology 47:1029-1031.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington Publication 242:1-512.

Clements, F. E. 1920. Plant indicators: the relation of plant communities to process and practice. Carnegie Institution of Washington Publication 290:1-388.

Clements, F. E. 1928. Plant succession and indicators. A definitive edition of plant succession and plant indicators. Wilson, New York. 453 pages.

Clements, F. E. 1936. Nature and structure of the climax. Journal of Ecology 24:252-284.

Climate Trends and Variations Bulletin for Canada. 2001. Annual 2001: Regional analysis. Environment Canada, Meteorological Service of Canada, Climate Research Branch. Web site http://www.msc-smc.ec.gc.ca/ccrm/bulletin/annual01/page2.htm. Accessed 04/02.

Collins, B. S., and S. T. A. Pickett. 1982. Vegetation composition and relation to environment in an Allegheny hardwoods forest. American Midland Naturalist 108:17-123.

Collins, B. S., K. P. Dunne, and S. T. A. Pickett. 1985. Responses of forest herbs to canopy gaps. Pages 217-234 *in* The Ecology of Natural Disturbances and Patch Dynamics (eds. S. T. A. Pickett and P. S. White). Academic Press, Inc. New York.

Collins, B. S., and S. T. A. Pickett. 1988a. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. Journal of Ecology 76:437-450.

Collins, B. S., and S. T. A. Pickett. 1988b Response of herb layer cover to experimental canopy gaps. American Midland Naturalist 119:282-290.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Cook, R. E., and E. E. Lyons. 1983. The biology of *Viola fimbriatula* in a natural disturbance. Ecology 64:654-660.

Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior and its development. Botanical Gazette 15:1-44, 115-140, 189-235.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2001. Canadian species at risk. November 2001. 38 pages. Web site http://www.cosewic.gc.ca/pdf/English/Full_List_Species_e.pdf. Accessed 04/02.

Curtis, H., and N. S. Barnes. 1989. Biology, 5th edition, Part 3: Biology of Populations. Worth Publishers, Inc. New York.

Damman, H., and M. L. Cain. 1998. Population growth and viability analyses of the clonal woodland herb, *Asarum canadense*. Journal of Ecology 86:13-26.

Davis, J. M. 1996. Advances in goldenseal cultivation. Horticultural Information Leaflet 131. North Carolina Cooperative Extension Service, Raleigh.

Davis, M. A., B. Ritchie, N. Graf, and K. Gregg. 1995. An experimental study of the effects of shade, conspecific crowding, pocket gophers and surrounding vegetation on survivorship, growth and reproduction in *Penstemon grandiflorus*. American Midland Naturalist 134:237-243.

Davison, S. E., and R. T. T. Forman. 1982. Herb and shrub dynamics in a mature oak forest: a thirty-year study. Bulletin of the Torrey Botanical Club 109:64-73.

Dawson, J. 1999. Eastern box turtle (*Terrapene carolina* L.). Web page http://theturtlepages.crosswinds.net/species/t_carolina/index.html. Accessed 04/02.

Dolman, P. M., and W. J. Sutherland. 1994. The use of soil disturbance in the management of Breckland grass heath. Journal of Environmental Management 41:123-140.

Ecological Stratification Working Group. 1995. A National Ecological Framework for Canada. Agriculture and Agri-food Canada, Research Branch, Centre for Land and Biological Resources Research and Environment Canada, State of the Environment Directorate, Ecozone Analysis Branch, Ottawa/Hull.

Eichenberger, M. D., and G. R. Parker. 1976. Goldenseal (*Hydrastis canadensis* L.) distribution, phenology, and biomass in an oak-hickory [Quercus-Carya ovata] forest. Ohio Journal of Science 76:204-210.

Fahselt, D. 1988. The dangers of transplantation as a conservation technique. Natural Areas Journal 8(4):238-244.

Falk, D. A., C. I. Millar, and M. Olwell (eds). 1996. Restoring diversity: strategies for reintroduction of endangered plants. Island Press, Washington, D.C.

Fetcher, N., and G. R. Shaver. 1983. Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. Journal of Ecology 71:131-147.

Foster, S. 1991. Goldenseal *Hydrastis canadensis*. Botanical Series Number 309. American Botanical Council, Austin. 8 pages.

Foster, S. 2000. Goldenseal, *Hydrastis canadensis*: goldenseal's future. Steven Foster Group. 5 pages. Web site http://www.herbphoto.com/education/monograph/goldenseal.html. Accessed 01/02.

Francis, C. M., M. J. W. Austen, and J. M. Bowles. 2000. Assessing floristic quality in southern Ontario woodlands. Natural Areas Journal 20(1):66-77.

Gagnon, D. 1999. A review of the ecology and population biology of goldenseal, and protocols for monitoring its populations: Final report to the Office of Scientific Authority of the US Fish and Wildlife Service. Groupe de recherce en écologie forestière Université du Québec, Montréal.

Ghosh, A. K., F. K. Bhattacharyya, and D. K. Ghosh. 1985. Leishmania donovani: Amastigote inhibition and mode of action of berberine. Experimental Parasitology 60:404-413.

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169-1194.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley, Chichester, UK.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52:107-145.

Gupte, S. 1975. Use of berberine in treatment of giardiasis. American Journal of Diseases of Children 129:866

Gysel, L. W. 1951. Borders and openings of beech-maple woodlands in southern Michigan. Journal of Forestry 49:13-19.

Hall, L. A. 1987. Transplantation of sensitive plants as mitigation for environmental impacts. Pages 413-420 *in* Conservation and Management of Rare and Endangered Plants: Proceedings of a California Conference on the Conservation and Management of Rare and Endangered Plants (ed. T. S. Elias). California Native Plant Society, Sacremento, California.

Hamon, N. W. 1990. Goldenseal. Herbal Medicine. November 1990:508-510.

Higgs, A. J., and M. B. Usher. 1980. Should nature reserves be large or small? Nature 285:568-569

Hilton-Taylor, C. (compiler). 2000. 2000 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland and Cambridge, UK. xviii+61 pp.

Holmgren, P. K., N. H. Holmgren, and L. C. Barnett. 1990. Index Herbariorum Part I: The Herbaria of the World. New York Botanical Garden, Bronx, New York. 693 pages.

Huang, W. 1990a. The role and mechanism of berberine on coronary arteries. Chung Hua Hsin Hsueh Kuan Ping Tsa Chih [Chinese Journal of Cardiology] 18:231-234.

Huang, W. 1990b. Ventricular tachyarrhythmias treated with berberine. Chung Hua Hsin Hsueh Kuan Ping Tsa Chih [Chinese Journal of Cardiology] 18:155-156,190.

Hughes, J. W. 1992. Effect of removal of co-occurring species on distribution and abundance of *Erythronium americanum* (Liliaceae), a spring ephemeral. American Journal of Botany 79:1329-1336.

Hughes, J. W., and T. J. Fahey. 1991. Colonization dynamics of herbs and shrubs in a disturbed northern hardwood forest. Journal of Ecology 79:605-616.

Hurkmans, M. E. 1995. Rare horsetails in trouble five years after transplanting (Ontario). Restoration and Management Notes 13(1):129.

Järvinen, O. 1982. Conservation of endangered plant populations: single large or several small reserves? Oikos 38:301-307.

Jax, K. 1999. Natürliche Störungen - ein wichtiges Konzept für Ökologie und Naturschutz? Z. Ökol. Natursch. 7:241-253.

Jenkins, M. A., and G. R. Parker. 1999. Composition and diversity of ground-layer vegetation in silvicultural openings of southern Indiana forests. American Midland Naturalist 142:1-16.

Jones, E. W. 1945. The structure and reproduction of the virgin forest of the North Temperate Zone. New Phytologist 44:130-148.

Kaneda, Y., T. Tanaka, and T. Saw. 1990. Effects of berberine, a plant alkaloid, on the growth of anaerobic protozoa in axenic culture. Tokai Journal of Experimental and Clinical Medicine 15:417-423.

Kaneda, Y., M. Torii, T. Tanaka, and M. Aikawa. 1991. In vitro effects of berberine sulphate on the growth and structure of Entamoeba histolytica, Giardia lamblia and Trichomonas vaginalis. Annals of Tropical Medicine and Parasitology 85:417-425.

Klinkhamer, P. G. L., and T. J. de Jong. 1988. The importance of small-scale disturbance for seedling establishment in *Cirsium vulgare* and *Cynoglossum officinale*. Journal of Ecology 76: 383-392.

Knapp, R. 1974. Vegetation Dynamics. Junk, The Hague.

Kotanen, P. M. 1997. Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. Canadian Journal of Botany 75:352-361.

Kumazawa, Y., A. Itagaki, M. Fukumoto, *et al.* 1984. Activation of peritoneal macrophages by berberine alkaloids in terms of induction of cytostatic activity. International Journal of Immunopharmacology 6:587-592.

Kurtén, B., and E. Anderson. 1980. Pleistocene mammals of North America. Columbia University Press, New York.

Lau, C. W., X. Q. Yao, Z. Y. Chen, W. H. Ko, and Y. Huang. 2001. Cardiovascular actions of berberine. Cardiovascular Drug Review 19(3):234-244.

Li, T. S. C., and A. Oliver. 1995. Specialty crops infosheet: Goldenseal. Province of British Columbia, Ministry of Agriculture, Fisheries and Food. Kamloops, British Columbia. 2 pages.

Lloyd, J. U., and C. G. Lloyd. 1884-1885. Drugs and Medicines of North America, Vol. 1, Ranunculaceae. Clarke, Cincinnati, OH. 304 pages.

Lloyd, J. U., and C. G. Lloyd. 1908. *Hydrastis canadensis*. Bulletin of the Lloyd Library of Botany, Pharmacy and Materia Medica 10. 184 pages. [Reproduction of portion of Lloyd and Lloyd 1884-1885, cited above.]

Mahajan, V. M., A. Sharma, and A. Rattan. 1982. Antimycotic activity of berberine sulphate: An alkaloid from an Indian medicinal herb. Sabouraudia 20:79-81.

Marin-Neto, J. A., B. C. Maciel, A. L. Secches, and L. Gallo Junior. 1988. Cardiovascular effects of berberine in patients with severe congestive heart failure. Clinical Cardiology 11:253-260.

Meagher, T. R. 1982. The population biology of *Chamaelirium luteum*, a dioecious member of the lily family: two-sex population projections and stable population structure. Ecology 63:1701-1711.

Menges, E. S. 1990. Population viability analysis for an endangered plant. Conservation Biology 4:52-62.

Messana, I, R. La Bua, and C. Galeffi. 1980. The alkaloids of *Hydrastis canadensis* L. (Ranunculaceae). Two new alkaloids: hydrastidine and isohydrastidine. Gazzetta Chimica Italiana 110: 539-543.

Metzger, F., and J. Schultz. 1981. Spring ground layer vegetation 50 years after harvesting in northern hardwood forests. American Midland Naturalist 105:44-50.

Miles, J. 1979. Vegetation Dynamics. Chapman and Hall, London.

Millspaugh, C. F. 1887. American medicinal plants; an illustrated and descriptive guide to the American plants uses as homeopathic remedies: their history, preparations, chemistry, and physiological effects. Boericke & Tafel, Philadelphia.

Moerman, D, E. 1986. Medicinal plants of native America. 2 vols. Technical Reports, No. 19, Research reports in Ethnobotany, Contribution 2. University of Michigan, Museum of Anthropology, Ann Arbor.

Mohan, M., C. R. Pant, S. K. Angra, and V. M. Mahajan. 1982. Berberine in trachoma. Indian Journal of Ophthalmology 30:69-75.

Moloney, K. A. 1988. Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. Ecology 69:1588-1598.

Moore, M. R., and J. L. Vankat.1986. Responses of the herb layer to the gap dynamics of a mature beech-maple forest. American Midland Naturalist 115:336-347.

Motten, A. F. 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecological Monographs 56:21-42.

Nakamoto K., S. Sadamori, and T. Hamada. 1990. Effects of crude drugs and berberine hydrochloride on the activities of fungi. Journal of Prosthetic Dentistry 64:691-694.

Nault, A., and D. Gagnon. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. Journal of Ecology 81:101-119.

Oldham, M. J., W. D. Bakowsky, and D. A. Sutherland. 1995. Floristic Quality Assessment System for Southern Ontario. Natural Heritage Information Centre, Ontario Ministry of Natural Resources, Peterborough, Ontario.

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). 1988. Soil Testing Methods Approved for Use in Ontario. Ontario Soil Management Committee. Ontario Ministry of Agriculture, Food and Rural Affairs, Ottawa.

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). 2000. Nursery and landscape plant production recommendations. Publication 383. Queen's Printer for Ontario, Ottawa.

Park, K. S., K. C. Kang, J. H. Kim, D. J. Adams, T. N. Johng, and Y. K. Paik. 1999. Differential inhibitory effects of protoberberines on sterol and chitin biosynthesis in *Candida albicans*. Journal of Antimicrobial Chemotherapy 43(5):667-674.

Pavlik, B. M., D. L. Nickrent, and A. M. Howald. 1993. The recovery of an endangered plant: I. Creating a new population of *Amsinckia grandiflora*. Conservation Biology 7(3):510-526.

Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107:238-248.

Pickett, S. T. A., and J. N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13:27-37.

Pickett, S. T. A., and P. S. White (eds.). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Inc., New York. 472 pages.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species association on badger disturbances in a tall-grass prairie. Ecological Monographs 45:285-305.

Primack, R. B. 1996. Lessons from ecological theory: dispersal, establishment, and population structure. Pages 209-233 *in* Restoring diversity: Strategies for Reintroduction of Endangered Plants (eds. D. A. Falk, C.I. Millar, and M. Olwell). Island Press, Washington, D.C.
Pyle, L. L. 1995. Effects of disturbance on herbaceous exotic plants species on the floodplain of the Potamac River. American Midland Naturalist 134:244-253.

Rabbani, G. H., T. Butler, J. Knight, *et al.* 1987. Randomized controlled trial of berberine sulfate therapy for diarrhea due to enterotoxigenic *Escherichia coli* and *Vibrio cholerae*. Journal of Infectious Diseases 155:979-984.

Rabinowitz, D., and J. K. Rapp. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. II. Detecting small-scale plant-to-plant interactions and separating disturbance from resource provision. American Journal of Botany 72:1629-1634.

Rapp, J. K., and D. Rabinowitz. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. I. Dynamics of forb and graminoid seedlings and shoots. American Journal of Botany 72:1618-1628.

Raup, H. M. 1941. Botanical problems in Boreal America. Botanical Review 7:147-248.

Reader, R. J., and B. D. Bricker. 1992. Response of five deciduous forest herbs to partial canopy removal and patch size. American Midland Naturalist 127:149-157.

Rehman, J., J. M. Dillow, S. M. Carter, J. Chou, B. Le, and A. S. Maisel. 1999. Increased production of antigen-specific immunoglobulins G and M following in vivo treatment with the medicinal plants *Echinacea angustifolia* and *Hydrastis canadensis*. Immunology Letters 68(2-3):391-395.

Reznicek, A. A. 1987. Are small reserves worthwhile for plants? Endangered Species Update 5(2):1-3.

Riccioppo, N. F. 1993. Electropharmacological effects of berberine on canine cardiac Purkinje fibres and ventricular muscle and atrial muscle of the rabbit. British Journal of Pharmacology 108:534-537.

Robbins, C. 1996. Goldenseal - a candidate for CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix II? TRAFFIC USA 15:5-6.

Rust, R. W., and R. R. Roth. 1981. Seed production and seedling establishment in the Mayapple, *Podophyllum peltatum* L. The American Midland Naturalist 105(1):51-60.

Rykiel, E. J. 1985. Towards a definition of disturbance. Australian Journal of Ecology 10:361-365.

Sabir, M., and N. K. Bhide. 1971. Study of some pharmacological actions of berberine. Indian Journal of Physiology and Pharmacology 15:111-132.

Sabir, M., V. M. Mahajan, L. N. Mohapatra, and N. K. Bhide. 1976. Experimental study of the antitrachoma action of berberine. Indian Journal of Medical Research 64:1160-1167.

Sack R. B., and J. L. Froehlich. 1982. Berberine inhibits intestinal secretory response of Vibrio cholerae and Escherichia coli enterotoxins. Infection and Immunity 35:471-475.
Scazzocchio, F., M. F. Cometa, L. Tomassini, and M. Palmery. 2001. Antibacterial activity of *Hydrastis canadensis* extract and its major isolated alkaloids. Planta Medica 67(6):561-564.

Schemske, D. W., M. F. Willson, M. N. Melampy, L. J. Miller, L. Verner, K. M. Schemske, and L. B. Best. 1978. Flowering ecology of some spring woodland herbs. Ecology 59(2):351-366.

Shideman, F. E. 1950. A review of the pharmacology and therapeutics of *Hydrastis* and its alkaloids, hydrastine, berberine, and canadine. Comm. on Nat. Formulary Bulletin (UK) 18(102):3-19.

Silvertown, J., M. Franco, and E. Menges. 1996. Interpretation of elasticity matrices as an aid to the management of plant populations for conservation. Conservation Biology 10(2):591-597.

Small, E., and P. M. Catling. 1999. Canadian Medicinal Crops. National Research Council of Canada, Ottawa. 240 pages.

Smith, R. L. 1990. Ecology and field biology, 4th ed. Harper Collins Publishers, New York. 922 pages.

Subbaiah, T. V., and A. H. Amin.1967. Effect of berberine sulphate on Entamoeba histolytica. Nature 215:527-528.

Sun, D., S. N. Abraham, E. H. Beachey. 1988a. Influence of berberine sulfate on synthesis and expression of Pap fimbrial adhesin in uropathogenic Escherichia coli. Antimicrobial Agents and Chemotherapy 32:1274-1277.

Sun, D., H. S. Courtney, and E. H. Beachey. 1988b. Berberine sulfate blocks adherence of Streptococcus pyogenes to epithelial cells, fibronectin, and hexadecane. Antimicrobial Agents and Chemotherapy 32:1370-1374.

Sutherland, W. J. (ed.). 1996. Ecological Census Techniques: a Handbook. Cambridge University Press, New York.

Swink, F. A., and G. S. Wilhelm. 1979. Plants of the Chicago region. Third edition. Morton Arboretum, Lisle, Illinois.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284-307.

Tardiff, S. E., and J. A. Stanford. 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology 79:2219-2228.

Thompson, J. N. 1980. Treefalls and colonization patterns of temperate forest herbs. American Midland Naturalist 104:176-184.

USFWS (United States Fish And Wildlife Service). 1997. Amendment to Appendix II of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), United States of America - Proposal to include *Hydrastis canadensis* in Appendix II, in accordance with Article 2, paragraph 2A.

Vasseur, L., and D. Gagnon. 1994. Survival and growth of *Allium tricoccum* Ait. transplants in different habitats. Biological Conservation 68:107-114.

Wagle, E. R., and G. A. Feldhamer. 1997. Feeding habits of the eastern woodrat (*Neotoma floridana*) in southern Illinois. Transactions of the Illinois State Academy of Science 90(3-4):171-177.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Weaver, J. E., and F. E. Clements. 1929. Plant Ecology. McGraw-Hill, New York. 520 pages.

Werner, P. A., and H. Caswell. 1977. Population growth rates and age versus stage-distribution for teasel (*Dipsacus sylvestris* Huds.). Ecology 58:1103-1111.

White, D. J. 1991. Status report on the Golden Seal, *Hydrastis canadensis*, in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review 45(3):229-299.

White, D. J., and H. L. Dickson. 1983. *Hydrastis canadensis* L. One page *in* Atlas of the rare vascular plants of Ontario, Part 2. (eds. G. W. Argus, and D. J. White). National Museum of Natural Sciences, Ottawa (looseleaf).

Whittaker, R. H. 1953. A consideration of the climax theory: the climax as a population and pattern. Ecological Monographs 22:1-44.

Wilhelm, G. S., and D. Ladd. 1988. Natural area assessment in the Chicago region. Transactions of the 53rd North American Wildlife and Natural Resources Conference:361-375.

Wilhelm, G. S., and L. A. Masters. 1995. Floristic quality assessment in the Chicago region and application computer programs. The Morton Arboretum, Lisle, Illinois.

Wu, J. F., and T. P. Liu. 1995. Effects of berberine on platelet aggregation and plasma levels of TXB2 and 6-keto-PGF1 alpha in rats with reversible middle cerebral artery occlusion. Yao Hsueh Hsueh Pao 30:98-102.

Xu, Z., H. Y. Cao, Q. Li. 1989. Protective effects of berberine on spontaneous ventricular fibrillation in dogs after myocardial infarction. Chung-Kuo Yao Li Hsueh Pao [ACTA Pharmacologica Sinica] 10:320-324.

Zar, J. H. 1984. Biostatistical Analysis, 2nd Edition. Prentice-Hall, Inc., New Jersey. 718 pages.

Zhang, M. F., and Y. Q. Shen. 1989. Antidiarrheal and anti-inflammatory effects of berberine. Chung Kuo Yao Li Hsueh Pao 10:174-176.

Zhu, B., and F. A. Ahrens. 1982. Effect of berberine on intestinal secretion mediated by Escherichia coli heat-stable enterotoxin in jejunum of pigs. Am J Vet Res 43:1594-1598.

Zwaving, J. H., and E. H. J. de Jong-Havenga. 1972. Determination of Hydrastine in Hydrastis fluid extract. Pharm. Weekblad 107:137-146.

Appendix A

Abbreviated Criteria for Evaluation of Species at Risk

Modified Table from Catling, P. M. 2001. Protecting vascular plant biodiversity in Canada: progress and problems with the taxon approach. Pages 62-81 *in* Bioconservation and Systematics: Proceedings of the Canadian Botanical Association Conference Symposium in London, Ontario, June 2000 (eds. J. B. Phipps and P. M. Catling). Canadian Botanical Association.

Abbreviated categories and criteria (from COSEWIC 2001). Any of the A-E criteria may give rise to endangered or threatened status, but the process of evaluation may be more complex in some cases than suggested by these guidelines.

	Endangered	**Threatened**	**Special Concern**
Criteria			
A. Declining Total Population	50% in 10 years or 3 generations	20% in 10 years or 3 generations	<20% in 10 years or 3 generations
B. Small Distribution and Decline or Fluctuation *Either* extent of occurrence *or* area of occupancy *and* any 2 of the following: (1) severely fragmented: or known to exist at # locations (2) continuing decline (3) fluctuation	 $<5{,}000$ km^2 <500 km^2 <6 any rate >1 order of magnitude	 $<20{,}000$ km^2 $<2{,}000$ km^2 <11 any rate >1 order of magnitude	 $>20{,}000$ km^2 $<2{,}000$ km^2 >10 any rate >1 order of magnitude
C. Small Total Population Size and Decline Number of mature individuals *and* of the following 2: (1) rapid decline rate of at *least* (2) continuing decline *and* either (a) fragmentation or (b) all individuals in a single population	 <2,500 20% in 5 years or 2 generations any rate all sub-populations <251	 <10,000 10% in 10 years or >3 generations any rate all sub-populations <1001	 >10,000 <10% in 10 years or > 3 generations any rate some sub-populations >1000
D. Very Small or Restricted *Either* (1) # mature individuals or (2) population is susceptible	 <250	 <1,000 and area of occupancy <100 km^2 or # locations <5	 >1,000 and area of occupancy >100 km^2 and # locations >5
E. Quantitative Analysis	20% in 10 years or 5 generations	10% in 100 years	

Special Concern: Those species which are particularly sensitive to human activities or natural events but are not endangered or threatened species. Examples of reasons why a species may qualify for "Special Concern": (1) a species that is particularly susceptible to a catastrophic event (e.g., a large seabird population near oil tanker route); (2) a conservation dependent species that would likely become at risk if not for active protection and management (e.g., a fish or mammal species protected from over-harvest); (3) a recovering species, no longer qualifying for risk categories but not yet clearly secure, or subject to resumption of threat in future. Examples of reasons why a species may not qualify for "Special Concern": (1) rarity alone in the absence of recognized threat; (2) threat with little possibility of serious harm (e.g., large, fecund population subject to harvest).

Appendix B
ANOVA Tables

One-Way ANOVAs

	SS	df	MS	F	R^2	*P*
Rhizome Volume						
treat	0.347	3	0.116	0.331	0.002	0.803
Rhizome Death 2000						
treat	0.060	3	0.020	0.155	0.001	0.926
Rhizome Death 2001						
treat	0.008	3	0.003	0.012	0.000	0.998
SeedDeath						
treat	0.250	3	0.083	0.373	0.007	0.773

Multi-Factor Non-Parametric ANOVAs

		SS	df	MS	H	Hc	R^2	*P*
	Biomass2000							
1	treat	77513.315	3	25837.772	5.83	5.84	0.409	0.120
	site	453028.894	4	113257.223	34.09	34.13		<0.001
	block(site)	1641946.731	95	17283.650	123.56	123.68		<0.026
	Error	3142793.560	297	10581.796				
2	treat	77513.315	3	25837.772	5.82	5.84	0.121	0.120
	site	453028.894	4	113257.223	34.01	34.13		<0.001
	treat x site	110851.716	12	9237.643	8.32	8.35		0.757
	Error	4673888.575	380	12299.707				
3	site	215931.303	4	53982.826	17.63	17.69	0.153	0.001
	PAR	392.746	1	392.746	0.032	0.032		0.858
	site x PAR	213655.706	4	53413.926	17.45	17.51		0.001
	Error	4358550.900	382	11409.819				
4	treat	37097.276	3	12365.759	2.84	2.85	0.023	0.415
	PAR	37539.476	1	37539.476	2.86	2.87		0.090
	treat x PAR	1920.458	3	640.153	0.15	0.15		0.986
	Error	5028118.046	384	13094.057				

		SS	df	MS	H	Hc	R^2	*P*
5	site	538342.558	4	134585.640	40.25	40.40	0.128	<<0.001
	treat	80510.661	3	26836.887	6.02	6.04		0.110
	PAR	118694.247	1	118694.247	8.87	8.90		0.003
	Error	4491695.945	383	11727.666				
	Biomass2001							
6	treat	30289.763	3	10096.588	2.38	2.45	0.395	0.484
	site	290045.442	4	72511.360	22.82	23.51		<0.001
	block(site)	1660068.808	94	17660.306	130.63	134.53		0.004
	Error	3039423.487	294	10338.175				
7	treat	36125.591	3	12041.864	2.88	2.97	0.095	0.396
	site	308798.466	4	77199.617	24.58	25.31		<<0.001
	treat x site	125835.562	12	10486.297	10.02	10.32		0.588
	Error	4478879.336	374	11975.613				
8	site	144172.919	4	36043.230	12.02	12.38	0.092	0.015
	PAR	2799.704	1	2799.704	0.23	0.24		0.624
	site x PAR	49495.370	4	12373.842	4.13	4.25		0.373
	Error	4493104.459	382	11762.054				
9	treat	25146.725	3	8382.242	19.92	20.52	0.017	<<0.001
	PAR	41461.028	1	41461.028	32.84	33.83		<<0.001
	treat x PAR	6949.477	3	2316.492	5.50	5.67		0.129
	Error	4861499.990	384	12660.156				
10	site	362319.518	4	90579.879	28.40	29.30	0.089	<<0.001
	treat	36469.880	3	12156.627	2.86	2.95		0.399
	PAR	97820.868	1	97820.868	7.67	7.90		0.005
	Error	4506129.949	383	11765.352				
11	treat	19355.019	3	6451.673	1.54	1.59	0.366	0.662
	biomass00	1728625.203	1	1728625.203	137.89	142.00		<<0.001
	treat x bio	41757.839	3	13919.280	3.33	3.43		0.330
	Error	3137011.261	386	8126.972				

		SS	df	MS	H	Hc	R^2	*P*
	Flowers2000							
12	treat	32573.235	3	10857.745	3.38	4.69	0.324	0.196
	site	190574.937	4	47643.734	19.79	27.46		<0.001
	block(site)	1022893.562	95	10767.301	106.20	147.38		<0.001
	Error	2597052.265						
13	treat	32573.235	3	10857.745	3.38	4.69	0.082	0.196
	site	190574.937	4	47643.734	19.79	27.46		<0.001
	treat x site	92430.277	12	7702.523	9.60	13.32		0.346
	Error	3527515.550	380	9282.936				
14	site	45623.187	4	11405.797	5.01	7.12	0.083	0.130
	PAR	718.377	1	718.377	0.08	0.11		0.740
	site x PAR	42962.064	4	10740.516	4.72	6.71		0.152
	Error	3473311.834	382	9092.439				
15	treat	29953.186	3	9984.395	3.09	4.40	0.027	0.221
	PAR	58228.228	1	58228.228	6.01	8.55		0.003
	treat x PAR	146228.364	3	5409.455	1.68	2.38		0.497
	Error	3682834.801	384	9590.716				
16	site	212047.262	4	53011.815	21.76	30.9	0.079	<<0.001
	treat	29257.995	3	9752.665	3.00	4.27		0.234
	PAR	92173.475	1	92173.475	9.46	13.45		<<0.001
	Error	3487015.903	383	9104.480				
17	treat	22467.495	3	7489.165	2.38	3.30	0.238	0.348
	biomass00	808026.385	1	808026.385	85.60	118.79		<<0.001
	treat x bio	6820.034	3	2273.345	0.72	1.00		0.801
	Error	2928928.993	392	7471.758				

		SS	df	MS	H	Hc	R^2	*P*
	Flowers2001							
18	treat	63067.423	3	21022.474	10.20	21.13	0.315	<<0.001
	site	71603.270	4	17900.818	11.58	23.84		<<0.001
	block(site)	630073.480	93	6774.984	101.86	210.98		<<0.001
	Error	1660042.327	291	5704.613				
19	treat	62712.545	3	20904.182	10.14	21.00	0.076	<0.001
	site	71603.270	4	17900.818	11.58	23.99		<<0.001
	treat x site	48443.056	12	4036.921	7.83	16.22		0.181
	Error	2241672.750	372	6026.002				
20	site	28688.815	4	7172.204	4.78	9.9	0.049	0.042
	PAR	11046.436	1	11046.436	1.84	3.8		0.051
	site x PAR	8425.245	4	2106.311	1.40	2.9		0.575
	Error	2305563.962	832	6035.508				
21	treat	15216.554	3	5072.185	2.51	5.20	0.030	0.158
	PAR	6897.029	1	6897.029	1.14	2.36		0.124
	treat x PAR	2974.755	3	991.585	0.49	1.01		0.799
	Error	2351847.292	384	6124.602				
22	site	103900.265	4	25975.066	16.58	34.34	0.072	<<0.001
	treat	63067.423	3	21022.474	10.06	20.84		<0.001
	PAR	39194.023	1	39194.023	5.97	12.37		<0.001
	Error	2250921.783	383	5877.080				
23	treat	10549.175	3	3516.392	1.76	3.64	0.187	0.303
	biomass00	365151.061	1	365151.061	60.90	126.15		<0.001
	treat x bio	2098.164	3	699.388	0.35	0.72		0.868
	Error	1972420.847	384	5136.513				
24	treat	2601.881	3	867.294	0.45	0.93	0.361	0.818
	biomass01	714582.441	1	714582.441	123.24	255.26		<0.001
	treat x bio01	6635.543	3	2211.848	1.14	2.37		0.499
	Error	1549157.463	384	4034.264				

		SS	df	MS	H	Hc	R^2	*P*
	Fruit2000							
25	treat	42416.135	3	14138.712	4.87	7.47	0.327	0.058
	site	136487.100	4	34121.775	15.67	24.05		<0.001
	block(site)	956832.775	95	10071.924	109.86	168.60		<0.001
	Error	2339351.490	297	7876.604				
26	treat	42416.135	3	14138.712	4.87	7.47	0.084	0.058
	site	136487.100	4	34121.775	15.67	24.05		<0.001
	treat x site	111946.715	12	9328.893	12.85	19.73		0.072
	Error	3184237.550	380	8379.573				
27	site	29960.544	4	7490.136	3.51	5.57	0.053	0.234
	PAR	3.067	1	3.067	0.0004	0.0006		0.980
	site x PAR	42516.464	4	10629.116	4.99	7.92		0.095
	Error	3261833.595	382	8538.831				
28	treat	9461.434	3	3153.811	1.09	1.72	0.021	0.632
	PAR	18882.590	1	18882.590	2.17	3.44		0.064
	treat x PAR	11057.904	3	3685.968	1.27	2.01		0.570
	Error	3369465.235	384	8774.649				
29	site	119454.850	4	29863.713	13.6	21.6	0.053	<0.001
	treat	43281.770	3	14427.257	4.9	7.8		0.050
	PAR	18672.839	1	18672.839	2.1	3.4		0.065
	Error	3261068.289	383	8514.539				
30	treat	19070.607	3	6356.869	2.27	3.48	0.299	0.323
	biomass00	884831.089	1	884831.089	105.20	161.45		<<0.001
	treat x bio00	15890811	3	5296.937	1.88	2.90		0.407
	Error	2436156.599	392	6214.685				

		SS	df	MS	H	Hc	R^2	*P*
	Fruit2001							
31	treat	55482.993	3	18494.331	11.85	32.45	0.317	<<0.001
	site	86981.991	4	21745.498	18.58	51.57		<<0.001
	block(site)	441013.831	94	4691.636	94.21	261.48		<<0.001
	Error	1260977.944	293	4303.679				
32	treat	57910.429	3	19303.476	12.41	34.44	0.108	<<0.001
	site	91174.637	4	22793.659	19.54	54.23		<<0.001
	treat x site	51408.116	12	4284.010	11.02	30.59		0.002
	Error	1637841.929	374	4379.256				
33	site	60072.887	4	15018.222	13.41	38.26	0.083	<<0.001
	PAR	260.294	1	260.294	0.06	0.17		0.685
	site x PAR	8469.010	4	2117.253	1.89	5.39		0.250
	Error	1682535.693	382	4404.544				
34	treat	16580.226	3	5526.742	3.61	10.30	0.043	0.016
	PAR	10070.500	1	10070.500	2.19	6.25		0.012
	treat x PAR	13398.609	3	4466.203	2.92	8.33		0.040
	Error	1755804.739	384	4572.408				
35	site	132580.764	4	33145.191	27.99	79.86	0.109	<<0.001
	treat	55174.000	3	18391.333	11.65	33.24		<<0.001
	PAR	50517.485	1	50517.485	10.66	30.43		<<0.001
	Error	1618706.715	383	4226.388				
36	site	133937.081	4	33484.270	28.58	81.55	0.116	<<0.001
	treat	16580.226	3	5526.742	3.54	10.1		0.018
	PAR	51034.285	1	51034.285	10.89	31.1		<<0.001
	treat x PAR	13398.609	3	4466.203	2.86	8.16		0.043
	Error	1621867.658	380	4268.073				

		SS	df	MS	H	Hc	R^2	*P*
37	treat	7889.020	3	2629.673	1.74	4.83	0.109	0.185
	biomass00	125126.876	1	125126.876	27.62	76.66		<<0.001
	treat x bio00	10296.501	3	3432.167	2.27	6.30		0.098
	Error	1636865.104	386	4240.583				
38	treat	1291.600	3	430.533	0.30	0.830	0.277	0.842
	biomass01	372802.221	1	372802.221	85.35	236.89		<<0.001
	treat x bio01	14292.335	3	4764.112	3.27	9.08		0.028
	Error	1328283.767	386	3441.150				
	# Seeds/Fruit							
39	treat	58455.901	3	19485.300	12.59	35.88	0.327	<<0.001
	site	94465.679	4	23616.420	20.35	58.83		<<0.001
	block(site)	443150.150	94	4714.363	265.61	767.88		<<0.001
	Error	1233206.849	293	4208.897				
40	treat	182.736	3	60.912	11.13	31.28	0.100	<<0.001
	site	327.095	4	81.774	19.92	55.99		<<0.001
	treat x site	141.129	12	11.761	8.59	24.14		0.019
	Error	5849.716	376	15.558				
41	site	62931.776	4	15732.944	13.94	41.5	0.088	<<0.001
	PAR	39.667	1	39.667	0.009	0.027		0.869
	site x PAR	9160.805	4	2290.201	2.05	6.10		0.192
	Error	1677207.882	382	4390.597				
42	treat	17051.180	3	5683.727	3.71	11.04	0.045	0.012
	PAR	11140.212	1	11140.212	2.43	7.23		0.007
	treat x PAR	11811.088	3	3937.029	2.57	7.65		0.054
	Error	1756114.556	384	4573.215				
43	site	140871.846	4	35217.962	29.4	87.5	0.115	<<0.001
	treat	59314.888	3	19771.629	12.4	36.9		<<0.001
	PAR	50903.007	1	50903.007	10.6	31.6		<<0.001
	Error	1627053.799	383	4248.182				

		SS	df	MS	H	Hc	R^2	*P*
44	treat	6809.729	3	2269.910	1.51	4.25	0.111	0.236
	biomass00	123627.329	1	123627.329	27.46	77.18		<<0.001
	treat x bio	11324.763	3	3774.921	2.52	7.07		0.070
	Error	1636515.816	388					
45	treat	704.867	3	234.956	0.16	0.47	0.279	0.925
	biomass01	362559.294	1	362559.294	83.45	241.25		<<0.001
	treat x bio	17881.827	3	5960.609	4.12	11.90		0.008
	Error	1326323.002	386	3436.070				
	Seedlings							
46	treat	1939.962	3	646.654	1.31	1.90	0.536	0.593
	site	47383.438	3	15794.479	32.04	46.52		<<0.001
	block(site)	76670.812	36	2129.745	51.85	75.28		<0.001
	Error	109122.788	117	932.673				
47	treat	1939.962	3	646.654	1.32	1.92	0.236	0.589
	site	47383.438	3	15794.479	32.25	46.80		<<0.001
	treat x site	6144.550	9	682.728	4.18	6.07		0.733
	Error	179649.050	144	1247.563				
48	site	4420.961	3	1473.654	3.68	5.34	0.218	0.149
	PAR	298.209	1	298.209	0.25	0.36		0.549
	site x PAR	2528.317	3	842.772	2.10	3.05		0.384
	Error	183907.170	152	1209.916				
49	treat	5670.149	3	1890.050	3.77	5.48	0.128	0.140
	PAR	21769.348	1	21769.348	14.49	21.04		<0.001
	treat x PAR	6481.942	3	2160.647	4.32	6.26		0.100
	Error	204925.747	152	1348.196				

		SS	df	MS	H	Hc	R^2	*P*
	Germination							
50	treat	1600.00	3	533.333	1.13	1.72	0.494	0.632
	site	39680.000	3	13226.667	28.09	42.68		<<0.001
	block(site)	69760.000	36	1937.778	49.38	75.02		<0.001
	Error	113600.000	117	970.940				
51	treat	1600.000	3	533.333	1.14	1.73	0.208	0.630
	site	39680.000	3	13226.667	28.26	42.94		<<0.001
	treat x site	5440.000	9	604.444	3.87	5.88		0.752
	Error	177920.000	144	1235.556				
52	site	4034.891	3	1344.964	3.40	5.17	0.190	0.160
	PAR	409.337	1	409.337	0.34	0.52		0.471
	site x PAR	2315.121	3	771.707	1.94	2.95		0.399
	Error	182067.781	152	1197.814				
53	treat	4045.984	3	1348.661	2.83	4.30	0.112	0.038
	PAR	18088.723	1	18088.723	12.67	19.24		<0.001
	treat x PAR	5360.812	3	1786.937	3.75	5.70		0.127
	Error	199590.465	152	1313.095				

Appendix C

Projection Matrices (Table 1) and Elasticity Matrices (Table 2)
for 14 Goldenseal Populations in Southwestern Ontario

Table1. Annual matrices, stable distribution vector (w), and growth rate (λ) for fourteen populations of goldenseal in southwestern Ontario.

	Class								
Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
1998 - 2000									
Pop. 1A									
seed	0	0	0	0	0	0	0	0	1.000
l	0	1.000	0.600	0.500	0	0	0	1.000	
L	0	0	0	0.080	0	0	0	0	
F	0	0	0.200	0.250	0	0	0	0	
V*l*	0	0	0	0.500	0	0	0	0	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	11.250	0	0	0	0	1.000
l	0	0.200	0	0	0	0	0	0	
L	0	0.600	1.000	0.250	0	0	0	0	
F	0	0.200	0	0.750	0	0	0	0	
V*l*	0	0.500	1.000	0	0.333	0	0	0	
VL	0	0.300	0	0	0.667	0	0	1.000	
VF	0	0	0	0	0	0	0	0	
Pop. 1B									
1998 - 2000									
seed	0	0	0	0	0	0	0	0	1.000
l	0	0.727	0.065	0	0	0	0	0	
L	0	0.182	0.677	0.500	0	0	0	0	
F	0	0.091	0.065	0.500	0	0	0	0	
V*l*	0	0	0.419	1.000	1.000	1.000	0	1.000	
VL	0	0	0.097	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
Pop. 2									
1998 - 2000									
seed	0	0	0	7.500	0	0	0	0.652	1.000
l	0	0.412	0.042	0	0	0	0	0	
L	0	0.353	0.375	0	0	0	0	0	
F	0	0.059	0.542	1.000	0	0	0	0.087	
V*l*	0	0.176	0.417	1.000	0.500	0	0	0.174	
VL	0	0	0.042	1.000	0	0	0	0.087	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	5.00	0	0	0	0	0.930
l	0	0.600	0.067	0	0	0	0	0	
L	0	0.200	0.533	0.125	0	0	0	0	
F	0	0	0.333	0.813	0	0	0	0	
V*l*	0	0.100	0.600	1.060	0.375	0	0	0.848	
VL	0	0	0.067	0.188	0.167	0	0	0.152	
VF	0	0	0	0	0	0	0	0	
Pop. 3									
1998 - 2000									
seed	0	0	0	0	0	0	0	0	1.000
l	0	0.304	0.071	0.161	0	0	0	0	
L	0	0	0.143	0	0	0	0	0	
F	0	0.043	0.357	0.613	0	0	0	0	
V*l*	0	0	0.214	0.452	1.000	0	0	0.875	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0.143	0	0	0.125	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
2000 - 2001									
seed	0	0	0	7.280	0	0	0	0	0.800
l	0	0.067	0	0	0	0	0	0	
L	0	0.333	0.500	0	0	0	0	1.000	
F	0	0.133	0	0.800	0	0	0	0	
V*l*	0	0	0	0.080	0.375	0	0	0	
VL	0	0	0	0.120	0.458	0	0	0	
VF	0	0	0	0	0	0	0	0	
Pop. 5									
1998 - 2000									
seed	0	0	0	1.670	0	0	0	0	0.816
l	0.133	0.722	0.350	0.111	0	0	0	0	
L	0	0.111	0.400	0	0	0	0	0	
F	0	0	0	0.333	0	0	0	0	
V*l*	0	0.222	0.300	0.333	0.667	0	0	1.000	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	3.000	0	0	0	0.750	1.000
l	0	0.870	0.100	0	0	0	0	0	
L	0	0.304	0.700	0	0	0	0	0	
F	0	0.043	0.200	1.000	0	0	0	0.250	
V*l*	0	0.087	0.300	0	0.533	0	0	0	
VL	0	0	0.100	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	

	Class								
Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
Pop. 6									
1998 - 2000									
seed	0	0	0	1.670	0	0	0	0	1.000
l	0.067	0.529	0.385	0.111	0	0	0	0	
L	0	0	0.462	0.222	0	0	0	0	
F	0	0.059	0.077	0.333	0	0	0	0	
V*l*	0	0.059	0	0	1.000	0	0	1.000	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	8.140	0	0	0	0.812	1.248
l	0	0.333	0	0	0	0	0	0.018	
L	0	0.267	0	0	0	0	0	0.004	
F	0	0.667	0.750	1.000	0	0	0	0.124	
V*l*	0	0.333	0.500	0.333	0	0	0	0.039	
VL	0	0.133	0.250	0	0	0	0	0.030	
VF	0	0	0.125	0	0	0	0	0	
Pop. 7									
1998 - 2000									
seed	0	0	0	15.000	0	0	0	0	0.793
l	0	0.444	0.174	0	0	0	0	0	
L	0	0.222	0.609	0.667	0	0	0	0	
F	0	0	0.087	0	0	0	0	0	
V*l*	0	0	0.217	1.000	0.727	0	0	0.897	
VL	0	0	0.043	0	0.091	0	0	0.103	
VF	0	0	0	0	0	0	0	0	

	Class								
Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
2000 - 2001									
seed	0	0	0	7.000	0	0	0	0	1.308
l	0.071	0.250	0.050	0	0	0	0	0	
L	0	1.000	0.450	0	0	0	0	0	
F	0.071	0.250	0.750	0.500	0	0	0	0	
V*l*	0	0.375	0	0	0.737	0.550	0	0.861	
VL	0	0	0.150	0.500	0.211	0	0	0.139	
VF	0	0	0	0	0	0	0	0	
Pop. 11									
1998 - 2000									
seed	0	0	0	10.000	0	0	0	0.731	1.061
l	0.022	0.250	0.100	0	0	0	0	0.029	
L	0.044	0.625	0.400	0	0	0	0	0.076	
F	0	0	0.400	0.667	0	0	0	0.078	
V*l*	0	0.625	0.300	0.111	0	0	0	0.047	
VL	0	0	0.111	0.222	0.333	0	0	0.039	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	10.000	0	0	0	0.849	1.012
l	0.020	0.600	0.143	0	0	0	0	0.046	
L	0	0	0.429	0.100	0	0	0	0.015	
F	0	0	0.071	1.000	0	0	0	0.086	
V*l*	0	0	0.214	0	0.100	0.333	0	0.004	
VL	0	0	0	0	0.100	0.333	0	0.001	
VF	0	0	0	0	0	0	0	0	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
Pop. 12									
1998 - 2000									
seed	0	0	0	10.710	0	0	0	0.496	0.952
l	0.053	0	0.182	0	0.444	0	0	0.123	
L	0	0.333	0.545	0.143	0	0	0	0.116	
F	0	0	0.091	0.714	0	0	0	0.044	
V*l*	0	0	0.727	0.286	0.333	0	0	0.156	
VL	0	0	0.182	0.143	0.111	0	0	0.047	
VF	0	0	0	0	0.111	0	0	0.018	
2000 - 2001									
seed	0	0	0	5.000	0	0	0	0	1.000
l	0	0.333	0	0	0	0	0	0	
L	0	0	0.300	0	0	0	0	0	
F	0	0	0.300	0.333	0	0	0	0	
V*l*	0	0	0.100	0.167	0.231	0.250	0	0	
VL	0	0	0	0	0.077	0	1.000	0	
VF	0	0	0	0	0	0	1.000	0	
Pop. 14									
1998 - 2000									
seed	0	0	0	10.000	0	0	0	0	1.000
l	0	0	0	0.500	0	0	0	0	
L	0	0	1.000	0.500	0	0	0	0	
F	0	0.500	0	0	0	0	0	0	
V*l*	0	0	0.667	0	0	0	0	0	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0.333	0	0	0	0	0	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
2000 - 2001									
seed	0	0	0	15.000	0	0	15.000	0	1.210
l	0.067	0.600	0.250	0	0	0	0	0	
L	0	0.200	1.000	0	0	0	0	0	
F	0	0.200	0	0.500	0	0	0	0	
V*l*	0	0.600	0.500	0	1.000	0	2.000	0	
VL	0	0	0	0	0	0	1.000	1.000	
VF	0	0.200	0	0	0	0	0	0	
Pop. 15									
1998 - 2000									
seed	0	0	0	15.000	0	0	0	0.500	1.000
l	0	0.667	0	0	0	0	0	0	
L	0	0.333	1.000	0	0	0	0	0	
F	0	0	0	1.000	0	0	0	0	
V*l*	0	0	0	0	0	0	0	0	
VL	0	0.333	0	0	0	0	0	0.500	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	4.000	0	0	0	0	1.000
l	0.250	0	0	0	0	0	0	0	
L	0	1.000	0.500	0	0	0	0	1.000	
F	0	0	0	1.000	0	0	0	0	
V*l*	0	0	0	0	0	1.000	0	0	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
Pop. 17									
1998 - 2000									
seed	0	0	0	10.000	0	0	0	0	0.917
l	0	0	0	0	0	0	0	0	
L	0	1.000	0.750	0.333	0	0	0	0	
F	0	0	0.125	0.667	0	0	0	0	
V*l*	0	1.000	0	0	0	0	0	0.647	
VL	0	0	0	0	0.500	0	0	0.353	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	15.330	0	0	0	0	0.667
l	0	0	0.250	0	0	0	0	1.000	
L	0	0	0.250	0.333	0	0	0	0	
F	0	0	0	0.667	0	0	0	0	
V*l*	0	0	0	0	0	0	0	0	
VL	0	0	0	0.333	0	0	0	0	
VF	0	0	0	0	0	0	0	0	
Pop. 18									
1998 - 2000									
seed	0	0	0	9.000	0	0	0	0	1.119
l	0	0	0.105	0	0	0	0	0	
L	0	0.636	0.316	0.500	0	0	0	0	
F	0	0	0.474	0.800	0	0	0	0	
V*l*	0	0.091	0.211	0	0.400	0	0	0.373	
VL	0	0	0	0	0.200	1.000	0	0.627	
VF	0	0	0	0	0	0	0	0	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
2000 - 2001									
seed	0	0	0	8.870	0	0	0	0	1.000
l	0	0.571	0	0	0	0	0	0	
L	0	0.143	0.875	0.462	0	0	0	0	
F	0	0.143	0	0.462	0	0	0	0	
V*l*	0	0	0	0.077	0.714	0	0	0	
VL	0	0	0	0	0.286	1.000	0	1.000	
VF	0	0	0	0	0	0	0	0	
Pop. 20									
1998 - 2000									
seed	0	0	0	0	0	0	0	0	0.721
l	0	0.674	0.314	0	0	0	0	0.729	
L	0	0.070	0.257	0.667	0	0	0	0.110	
F	0	0	0	0	0	0	0	0	
V*l*	0	0.020	0.171	0	0.500	0	0	0.161	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	
2000 - 2001									
seed	0	0	0	0	0	0	0	0	0.754
l	0	0.500	0.143	0	0	0	0	0.270	
L	0	0.325	0.571	0	0	0	0	0.479	
F	0	0	0	0	0	0	0	0	
V*l*	0	0.025	0.143	0	0.455	0	0	0.252	
VL	0	0	0	0	0	0	0	0	
VF	0	0	0	0	0	0	0	0	

Class	seed	*l*	L	F	V*l*	VL	VF	w	λ
Overall									
1998 - 2000									
seed	0	0	0	15	0	0	0	0.622	0.889
l	0.025	0.497	0.180	0.151	0	0	0	0.081	
L	0.009	0.185	0.438	0.161	0	0	0	0.059	
F	0	0.029	0.180	0.538	0	0	0	0.037	
V*l*	0	0.098	0.309	0.409	0.603	0.333	0	0.172	
VL	0	0.006	0.032	0.054	0.074	0.167	0	0.024	
VF	0	0	0.005	0	0.029	0	0	0.006	
2000 - 2001									
seed	0	0	0	5.125	0	0	0	0.000	0.927
l	0.013	0.433	0.071	0	0	0	0	0.000	
L	0	0.312	0.407	0.148	0	0	0	0.000	
F	0.004	0.121	0.236	0.784	0	0	0	0.000	
V*l*	0	0.153	0.257	0.261	0.360	0.136	1.000	0.193	
VL	0	0.038	0.050	0.114	0.168	0.182	1.000	0.807	
VF	0	0.006	0.007	0	0	0	0.500	0.000	

Table 2. Elasticity matrices and reproductive value vector (v) for annual and mean transition matrices for fourteen populations of *Hydrastis canadensis* in southwestern Ontario.

	Class							
Class	seed	*l*	L	F	V*l*	VL	VF	v
Pop. 1A								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	1.000	0	0	0	0	0	0.400
L	0	0	0	0	0	0	0	0.300
F	0	0	0	0	0	0	0	0.300
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.333
L	0	0	0	0	0	0	0	0.333
F	0	0	0	0	0	0	0	0.333
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
Pop. 1B								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.276
L	0	0	0	0	0	0	0	0.232
F	0	0	0	0	0	0	0	0.362
V*l*	0	0	0	0	1.000	0	0	0.065
VL	0	0	0	0	0	0	0	0.065
VF	0	0	0	0	0	0	0	0

Class	Class seed	*l*	L	F	V*l*	VL	VF	v
Pop. 2								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.253
L	0	0	0	0	0	0	0	0.356
F	0	0	0	1.000	0	0	0	0.391
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0	0	0	0	0
l	0	0.005	0.002	0	0	0	0	0.227
L	0	0.002	0.033	0.022	0	0	0	0.374
F	0	0	0.022	0.151	0	0	0	0.400
V*l*	0	0	0	0	0.193	0	0	0
VL	0	0	0	0	0.285	0	0	0
VF	0	0	0	0	0	0	0	0
Pop. 3								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.024
L	0	0	0	0	0	0	0	0.249
F	0	0	0	0	0	0	0	0.396
V*l*	0	0	0	0	1.000	0	0	0.330
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0

	Class							
Class	seed	*l*	L	F	V*l*	VL	VF	v
2000 - 2001								
seed	0	0	0	66.248	0	0	0	0
l	0	0.006	0	0	0	0	0	0.154
L	0	0.139	0.313	0	0	0	0	0
F	0	0.022	0	0.800	0	0	0	0.846
V*l*	0	0	0	0.008	0.176	0	0	0
VL	0	0	0	0.018	0.262	0	0	0
VF	0	0	0	0	0	0	0	0
Pop. 5								
1998 - 2000								
seed	0	0	0	3.420	0	0	0	0
l	0.022	0.639	0.150	0.015	0	0	0	0
L	0	0.015	0.196	0	0	0	0	0
F	0	0	0	0.136	0	0	0	1.000
V*l*	0	0.060	0.110	0.136	0.546	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0	0	0	0	0
l	0	0.595	0.069	0	0	0	0	0.585
L	0	0.089	0.207	0	0	0	0	0.250
F	0	0	0	0	0	0	0	0
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0.020	0	0	0	0	0.165
VF	0	0	0	0	0	0	0	0

	Class							
Class	seed	*l*	L	F	V*l*	VL	VF	v
Pop. 6								
1998 - 2000								
seed	0	0	0	0	0	0	0	0.007
l	0	0	0	0	0	0	0	0.102
L	0	0	0	0	0	0	0	0.081
F	0	0	0	0	0	0	0	0.061
V*l*	0	0	0	0	1.000	0	0	0.749
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0.148	0	0	0	0.012
l	0.070	0.026	0	0	0	0	0	0.357
L	0	0.014	0	0	0	0	0	0.237
F	0.078	0.057	0.014	0.595	0	0	0	0.394
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
Pop. 7								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.257
L	0	0	0	0	0	0	0	0.404
F	0	0	0	0	0	0	0	0.340
V*l*	0	0	0	0	0.904	0	0	0
VL	0	0	0	0	0.082	0	0	0
VF	0	0	0	0	0	0	0	0

Class	seed	*l*	L	F	V*l*	VL	VF	v
2000 - 2001								
seed	0	0	0	0.020	0	0	0	0.036
l	0.011	0.003	0.001	0	0	0	0	0.354
L	0	0.009	0.005	0	0	0	0	0.296
F	0.010	0.002	0.008	0.013	0	0	0	0.314
V*l*	0	0	0	0	0.485	0.058	0	0
VL	0	0	0	0	0.058	0	0	0
VF	0	0	0	0	0	0	0	0
Pop. 11								
1998 - 2000								
seed	0	0	0	0.165	0	0	0	0.017
l	0.046	0.021	0.022	0	0	0	0	0.234
L	0.119	0.068	0.113	0	0	0	0	0.304
F	0	0	0.165	0.280	0	0	0	0.444
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0
L	0	0	0.009	0.012	0	0	0	0.109
F	0	0	0.012	0.968	0	0	0	0.891
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0

Class	seed	*l*	L	F	V*l*	VL	VF	v
Pop. 12								
1998 - 2000								
seed	0	0	0	0.034	0	0	0	0.060
l	0.034	0	0.027	0	0.089	0	0	0.103
L	0	0.150	0.232	0.023	0	0	0	0.295
F	0	0	0.069	0.206	0	0	0	0.523
V*l*	0	0	0.077	0.012	0.048	0	0	0.074
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	25.000	0	0	0	0
l	0	0.111	0	0	0	0	0	0
L	0	0	0.090	0	0	0	0	0
F	0	0	0.090	0.111	0	0	0	0
V*l*	0	0	0.010	0.028	0.053	0.063	0	0
VL	0	0	0	0	0.006	0	1.000	0
VF	0	0	0	0	0	0	1.000	0
Pop. 14								
1998 - 2000								
seed	0	0	0	100.000	0	0	0	0
l	0	0	0	0.250	0	0	0	0
L	0	0	1.000	0.250	0	0	0	0
F	0	0.250	0	0	0	0	0	0
V*l*	0	0	0.445	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0.111	0	0	0	0	0

	Class							
Class	seed	*l*	L	F	V*l*	VL	VF	v
2000 - 2001								
seed	0	0	0	185.985	0	0	185.985	0.013
l	0.004	0.298	0.052	0	0	0	0	0.244
L	0	0.033	0.827	0	0	0	0	0.290
F	0	0.033	0	0.207	0	0	0	0.285
V*l*	0	0.298	0.207	0	0.827	0	3.306	0
VL	0	0	0	0	0	0	0.827	0
VF	0	0.033	0	0	0	0	0	0.167
Pop. 15								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0
L	0	0	0	0	0	0	0	0
F	0	0	0	0	0	0	0	0.500
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0.500
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	16.000	0	0	0	0
l	0.063	0	0	0	0	0	0	0
L	0	1.000	0.250	0	0	0	0	0
F	0	0	0	1.000	0	0	0	1.000
V*l*	0	0	0	0	0	1.000	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0

	Class							
Class	seed	*l*	L	F	V*l*	VL	VF	v
Pop. 17								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.278
L	0	0	0	0	0	0	0	0
F	0	0	0	0	0	0	0	0
V*l*	0	0	0	0	0	0	0	0.255
VL	0	0	0	0	0.500	0	0	0.467
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	352.337	0	0	0	0
l	0	0	0.094	0	0	0	0	0
L	0	0	0.094	0.166	0	0	0	0.294
F	0	0	0	0.667	0	0	0	0
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0.166	0	0	0	0.706
VF	0	0	0	0	0	0	0	0
Pop. 18								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.181
L	0	0	0	0	0	0	0	0.319
F	0	0	0	0	0	0	0	0.500
V*l*	0	0	0	0	0.051	0	0	0
VL	0	0	0	0	0.091	0.767	0	0
VF	0	0	0	0	0	0	0	0

	Class							
Class	seed	*l*	L	F	V*l*	VL	VF	v
2000 - 2001								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0.022
L	0	0	0	0	0	0	0	0
F	0	0	0	0	0	0	0	0.065
V*l*	0	0	0	0	0	0	0	0.456
VL	0	0	0	0	0	1.000	0	0.456
VF	0	0	0	0	0	0	0	0
Pop. 20								
1998 - 2000								
seed	0	0	0	0	0	0	0	0
l	0	0	0	0	0	0	0	0
L	0	0	0	0	0	0	0	0
F	0	0	0	0	0	0	0	1.000
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0	0	0	0	0
l	0	0.278	0.141	0	0	0	0	0.561
L	0	0.141	0.440	0	0	0	0	0.439
F	0	0	0	0	0	0	0	0
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0

Class	Class							
	seed	*l*	L	F	V*l*	VL	VF	v
Overall								
1998 - 2000								
seed	0	0	0	0.087	0	0	0	0.080
l	0.055	0.142	0.037	0.020	0	0	0	0.173
L	0.032	0.086	0.149	0.034	0	0	0	0.283
F	0	0.026	0.115	0.216	0	0	0	0.536
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0
2000 - 2001								
seed	0	0	0	0.049	0	0	0	0.060
l	0.032	0.039	0.013	0	0	0	0	0.273
L	0	0.026	0.068	0.061	0	0	0	0.251
F	0.017	0.019	0.074	0.602	0	0	0	0.470
V*l*	0	0	0	0	0	0	0	0
VL	0	0	0	0	0	0	0	0
VF	0	0	0	0	0	0	0	0

Appendix D

Data used in Section 2.3: Ecological Aspects

Number of stems (small, large, flowering, and fruiting), number and cover of plant associates, and soil chemistry within quadrats as well as number of stems and patches, natural area size, habitat size, and disturbance value for each site.

SITE	QSTEMS	QSMALL	QBIG	QFLOW	QFRUIT	QDIV	PH	NA	P	K
1	18	1	5	12	0	7	6.3	129	14	140
2	55	21	32	2	2	10	6.4	80	8	176
3	50	23	25	2	1	5	7.5	73	9	179
4	75	30	14	31	0	8	6.3	72	7	100
5	51	21	24	6	6	9	6.1	76	11	149
6	50	21	20	9	1	13	6.1	81	12	93
7	41	19	13	9	1	12	5.7	77	12	123
8	31	8	16	7	7	8	5.4	73	10	72
9	73	38	17	18	1	3				
10	45	14	19	12	5	5				
11	70	38	17	15	6	7				
12	30	11	10	9	6	9				
13	36	18	11	7	5	9				
14	123	76	31	16	11	7				
15	7	2	3	2	2	12				
16	6	3	1	2	2	11	5.7	90	11	73
17	52	25	17	10	1	7	7.8	74	14	141
18	15	3	9	3	2	6	7.4	73	12	230
19	41	16	20	5	3	9	7.8	81	7	77
20	92	54	35	3	0	7	7.3	62	30	114

SITE	QCOVER	STEMS	NATSIZE	HABSIZE	DVALUE	GPATCH	MG	CA	ZN	OM
1	91	1153	10.1	0.062	3	8	266	2270	27	9.66
2	107.5	768	10.1	0.017	5	11	323	2780	43	8.78
3	82	106	13.5	0.131	2	1	528	8240	26	12.1
4	71	4329	29.1	0.254	5	9	300	2730	26	8.2
5	86.5	455	59.2	0.289	1	3	114	1290	30	7.99
6	127	1980	75.1	0.121	1	1	221	2360	60	9.44
7	52	2597	48.8	0.452	2	9	375	2710	48	11.11
8	183	45	11	0.146	1	1	290	2420	29	5.75
9	21	283	7.9	0.059	2	5				
10	43	165	35.9	0.316	5	2				
11	106.5	640	2.7	0.026	3	6				
12	115	203	253.6	1.175	2	3				
13	175	45	253.6	1.175	1	1				
14	104	261	253.6	1.15	1	1				
15	71.5	10	253.6	1.15	1	1				
16	106.5	188	52.1	0.3	2	2	100	1420	33	5.93
17	32.5	440	457.4	0.071	3	3	257	7350	29	13.49
18	58	37	457.4	0.363	1	2	191	8300	36	23.13
19	34	241	199.6	0.022	1	1	169	6960	18	10.72
20	35.5	648	90.1	0.115	5	5	203	3990	30	6.94

VARIABLES

QSTEMS = # stems in quadrat
QSMALL = # small stems in quadrat
QBIG = # large stems in quadrat
QFLOW = # flowering stems in quadrat
QFRUIT = # fruiting stems in quadrat
QDIV = # plant associates in quadrat
QCOVER = cover of plant associates in quadrat (%)

STEMS = # stems at a site
NATSIZE = natural area size (ha)
HABSIZE = habitat size (km2)
DVALUE = disturbance value (%)
GPATCH = # goldenseal patches at a site
OM = organic matter (%)

Appendix E

Transplant Data from Experiment

Variables:

SITE
BLOCK
TREAT = treatment; C = control, F = fertilization, D = soil turnover,
FD = fertilization + soil turnover
00 = data from 2000
01 = data from 2001
RVOLUME = rhizome volume, cm^3
BIOMASS = biomass, cm^2
RDEATH = rhizome mortality in 2000; 0 = survived, 1 = died
PAR = photosynthetically active radiation, $\mu E/cm^2 sec$
STEMS = number of stems
FLOWER= number of flowers
FRUIT = number of fruit
TSEEDS = number of seeds per fruit

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
1	161	C	0.667	340.25825	0	269.412	0
1	161	FD	0.667	462.7104	0	370.7084	0
1	161	D	1.256	986.3368	0	275.849	0
1	161	F	0.805	417.9654	0	649.1165	0
1	150	D	0.678	168.18625	0	118.1425	0
1	150	C	0.184	0	1	0	1
1	150	FD	0.667	198.291	0	368.32985	0
1	150	F	0.49	222.626	0	302.225	0
1	142	D	0.864	394.07	0	0	1
1	142	C	0.726	445.409	0	495.806	0
1	142	F	0.628	0	1	0	1
1	142	FD	0.569	581.20615	0	908.402	0
1	143	D	0.726	498.9774	0	382.17725	0
1	143	FD	0.628	469.65765	0	0	1
1	143	F	0.491	432.535	0	73.947	0
1	143	C	0.201	86.978	0	0	1
1	149	C	0.726	0	1	0	1
1	149	F	1.074	248.374	0	0	1
1	149	D	0.648	498.0354	0	446.2725	0
1	149	FD	0.301	387.005	0	38.622	0
1	144	FD	1.962	643.8884	0	929.44	0
1	144	C	1.021	425.85465	0	319.966	0
1	144	F	0.402	192.639	0	59.35385	0
1	144	D	0.844	434.105	0	519.827	0
1	146	FD	1.215	567.28025	0	409.927	0
1	146	C	0.608	392.41365	0	410.869	0
1	146	D	0.471	387.67225	0	0	1
1	146	F	0.451	359.53	0	0	1
1	141	FD	0.314	237.42325	0	0	1
1	141	F	0.414	361.1	0	664.738	0
1	141	C	0.276	269.412	0	479.5094	0
1	141	D	3.316	490.19325	0	816.43925	0
1	162	D	0.876	620.1814	0	0	1
1	162	C	0.264	153.89925	0	0	1
1	162	FD	0.628	144.911	0	0	1
1	162	F	0.452	133.293	0	83.4926	0
1	166	C	0.824	335.666	0	417.18825	0
1	166	FD	0.334	298.0174	0	0	1
1	166	F	0.648	0	1	0	1
1	166	D	1.215	0	1	0	1
1	160	D	0.477	373.8484	0	144.44	0
1	160	F	1.554	447.8739	0	0	1
1	160	FD	1.217	485.35765	0	0	1
1	160	C	0.301	0	1	0	1
1	158	C	0.962	612.3314	0	601.153	0
1	158	F	0.138	125.286	0	106.289	0
1	158	D	0.301	494.2674	0	585.36665	0
1	158	FD	0.412	24.84525	0	0	1
1	151	F	0.51	421.702	0	0	1
1	151	C	0.942	902.1534	0	591.861	0
1	151	FD	0.201	166.106	0	0	1
1	151	D	0.471	371.0224	0	533.172	0
1	154	FD	0.451	384.53225	0	850.19425	0
1	154	F	1.23	63.78125	0	0	1
1	154	D	0.608	781.14565	0	244.17425	0
1	154	C	0.471	331.427	0	102.992	0
1	153	FD	0.432	272.238	0	67.07825	0
1	153	D	0.593	381.196	0	0	1

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
1	153	F	1.272	334.567	0	331.59185	0
1	153	C	0.427	299.399	0	0	1
1	159	D	0.628	411.5284	0	0	1
1	159	F	0.667	36.738	0	0	1
1	159	C	0.608	574.62	0	0	1
1	159	FD	0.432	410.1154	0	430.18	0
1	167	F	0.188	175.526	0	0	1
1	167	FD	2.116	789.3018	0	0	1
1	167	C	0.726	322.3524	0	370.991	0
1	167	D	0.707	246.647	0	73.1149	0
1	168	D	0.765	362.5444	0	686.7494	0
1	168	FD	0.432	527.5514	0	527.40225	0
1	168	F	0.628	509.1824	0	838.0346	0
1	168	C	0.236	279.6484	0	62.55665	0
1	169	C	0.844	303.167	0	730.05	0
1	169	F	1.276	392.8454	0	635.065	0
1	169	FD	1.5	119.83025	0	198.95825	0
1	169	D	0.628	790.44005	0	384.53225	0
1	145	FD	0.301	0	1	0	1
1	145	F	0.54	371.68665	0	11.775	0
1	145	D	0.824	542.3094	0	804.47585	0
1	145	C	0.922	305.993	0	437.75525	0
2	59	FD	1	546.3914	0	23.2046	0
2	59	F	1.433	402.548	0	0	1
2	59	C	1.752	33.95125	0	0	1
2	59	D	0.608	0	1	0	1
2	60	F	1.231	297.5464	0	86.036	0
2	60	D	0.726	405.28765	0	430.25065	0
2	60	FD	0.691	142.085	0	18.06285	0
2	60	C	1.046	94.514	0	0	1
2	61	D	0.289	124.344	0	507.581	0
2	61	FD	0.364	90.97365	0	59.189	0
2	61	F	0.791	111.941	0	0	1
2	61	C	0.791	110.057	0	0	1
2	62	FD	0.162	53.89025	0	24.806	0
2	62	F	1.158	317.6424	0	330.3594	0
2	62	C	1.158	145.9315	0	0	1
2	62	D	0.414	240.995	0	0	1
2	64	C	0.883	273.18	0	598.641	0
2	64	FD	0.54	273.18	0	434.2934	0
2	64	D	1.272	333.782	0	762.706	0
2	64	F	1.356	490.8134	0	731.934	0
2	65	D	0.264	245.705	0	398.78	0
2	65	F	0.402	313.28565	0	0	1
2	65	C	1.441	7.379	0	0	1
2	65	FD	0.465	241.937	0	536.469	0
2	67	F	0.49	196.4384	0	473.826	0
2	67	C	0.364	0	1	0	1
2	67	D	3.467	0	1	0	1
2	67	FD	1.074	60.602	0	0	1
2	66	F	0.327	241.937	0	711.3356	0
2	66	D	1.017	265.644	0	685.148	0
2	66	C	0.373	275.8804	0	149.3384	0
2	66	FD	0.628	335.509	0	663.796	0
2	63	FD	0.707	149.621	0	133.01825	0
2	63	D	0.314	52.595	0	0	1
2	63	C	0.452	336.6394	0	163.6254	0
2	63	F	0.294	191.45365	0	72.063	0

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
2	70	C	0.55	266.6174	0	326.246	0
2	70	D	0.465	335.6974	0	757.996	0
2	70	F	0.377	191.2288	0	0	1
2	70	FD	1.102	332.84	0	1095.0436	0
2	69	D	0.465	133.96025	0	0	1
2	69	F	1.187	0	1	0	1
2	69	FD	1.272	0	1	0	1
2	69	C	0.414	0	1	0	1
2	68	C	0.648	253.1154	0	531.17025	0
2	68	D	0.904	0	1	0	1
2	68	FD	1.074	63.428	0	0	1
2	68	F	0.746	0	1	0	1
2	71	FD	0.864	280.716	0	658.34025	0
2	71	C	0.883	0	1	0	1
2	71	F	1.356	235.814	0	528.03025	0
2	71	D	0.82	638.8644	0	88.6265	0
2	72	D	2.154	45.059	0	122.46	0
2	72	F	1.356	0	1	0	1
2	72	C	0.364	0	1	0	1
2	72	FD	0.301	59.66	0	162.6834	0
2	73	F	0.301	0	1	0	1
2	73	FD	1.046	147.737	0	420.7286	0
2	73	D	0.51	266.272	0	578.074	0
2	73	C	0.569	0	1	0	1
2	74	F	2.308	121.518	0	433.163	0
2	74	FD	1.731	637.42	0	472.884	0
2	74	D	0.883	125.286	0	0	1
2	74	C	0.569	126.228	0	331.427	0
2	77	C	1.667	222.173	0	283.411	0
2	77	FD	0.569	25.277	0	42.58625	0
2	77	F	0.667	0	1	0	1
2	77	D	0.569	67.667	0	129.996	0
2	78	FD	1.217	204.571	0	560.5214	0
2	78	F	0.201	46.158	0	0	1
2	78	C	0.667	58.718	0	190.755	0
2	78	D	0.707	77.715	0	0	1
2	79	D	2.612	0	1	0	1
2	79	F	0.276	0	1	0	1
2	79	C	1.616	125.286	0	300.341	0
2	79	FD	0.314	167.99	0	398.78	0
2	80	FD	0.942	327.38425	0	669.448	0
2	80	C	1.04	189.813	0	0	1
2	80	F	0.201	46.001	0	0	1
2	80	D	0.412	242.879	0	527.834	0
3	138	D	0.353	197.2234	0	316.39425	0
3	138	C	0.251	55.7036	0	124.54025	0
3	138	F	1.243	621.406	0	1017.36	0
3	138	FD	0.933	142.0379	0	125.29385	0
3	98	FD	1.017	664.424	0	1328.165	0
3	98	C	0.667	270.2755	0	146.1984	0
3	98	F	0.414	183.5644	0	0	1
3	98	D	0.569	274.00425	0	404.6204	0
3	133	C	1.526	243.821	0	631.99565	0
3	133	F	1.423	631.297	0	609.32485	0
3	133	D	0.707	559.7364	0	834.71405	0
3	133	FD	0.726	667.32065	0	1419.437	0
3	132	FD	0.666	309.4784	0	542.1995	0
3	132	C	0.412	388.1354	0	437.716	0

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
3	132	D	0.491	345.4314	0	428.64925	0
3	132	F	0.502	426.76525	0	341.51425	0
3	131	D	0.412	383.4254	0	538.58065	0
3	131	FD	0.628	345.243	0	348.9796	0
3	131	F	0.942	0	1	0	1
3	131	C	0.55	561.1494	0	1031.8825	0
3	91	FD	1.616	0	1	0	1
3	91	C	0.824	0	1	0	1
3	91	F	0.099	0	1	0	1
3	91	D	2.039	0	1	0	1
3	86	FD	1.021	280.402	0	893.4085	0
3	86	D	0.805	0	1	0	1
3	86	C	1.159	0	1	0	1
3	86	F	1.099	0	1	0	1
3	99	C	0.648	172.89625	0	300.812	0
3	99	F	2.883	636.949	0	411.9052	0
3	99	D	0.188	65.94785	0		1
3	99	FD	0.65	0	1		1
3	100	FD	0.846	0	1		
3	100	F	1.692	0	1		
3	100	D	0.883	166.891	0		
3	100	C	0.667	0	1		
3	96	FD	0.904	695.0704	0	770.3519	0
3	96	F	0.471	332.84	0	672.5095	0
3	96	D	1.413	893.36925	0	528.81525	0
3	96	C	0.353	418.75825	0	704.8986	0
3	81	F	0.201	124.344	0	382.17725	0
3	81	C	0.201	135.84425	0	286.6506	0
3	81	FD	0.44	0	1	0	1
3	81	D	0.569	0	1	0	1
3	94	FD	0.989	605.078	0	930.26425	0
3	94	D	0.451	129.95675	0	827.39	0
3	94	F	0.589	306.2599	0	498.632	0
3	94	C	0.59	298.457	0	514.175	0
3	82	C	0.251	144.911	0	365.025	0
3	82	F	0.251	281.5324	0	322.321	0
3	82	FD	0.961	83.21	0	0	1
3	82	D	0.864	872.92	0	782.017	0
3	90	F	0.214	0	1	0	1
3	90	D	0.728	138.04225	0	174.0816	0
3	90	C	1.846	0	1	0	1
3	90	FD	0.864	494.2674	0	701.162	0
3	137	D	0.477	227.84625	0	629.413	0
3	137	FD	1.808	166.106	0	366.44585	0
3	137	F	1.3	455.0174	0	765.846	0
3	137	C	0.65	285.3004	0	484.22725	0
3	88	F	0.106	171.2085	0	272.7404	0
3	88	D	0.608	644.71265	0	931.7793	0
3	88	FD	0.707	503.656	0	990.8741	0
3	88	C	0.352	350.424	0	405.7194	0
3	89	C	0.569	365.967	0	725.4656	0
3	89	D	0.765	0	1	0	1
3	89	FD	0.451	291.5176	0	489.526	0
3	89	F	0.471	536.35125	0	787.355	0
3	87	F	1.578	0	1	0	1
3	87	D	0.824	431.6244	0	958.642	0
3	87	C	1.808	147.737	0	318.5216	0
3	87	FD	1.611	0	1	0	1

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
3	95	C	3.039	663.168	0	1175.1764	0
3	95	F	0.264	419.818	0	862.715	0
3	95	D	0.962	0	1	0	1
3	95	FD	0.276	0	1	0	1
3	97	FD	1.046	464.877	0	277.30125	0
3	97	C	1.554	561.903	0	468.05625	0
3	97	F	0.477	28.26	0	230.67225	0
3	97	D	0.353	469.15525	0	695.6984	0
4	112	D	1.138	167.99	0	470.058	0
4	112	C	0.961	95.927	0	204.13925	0
4	112	F	0.765	346.3734	0	469.2259	0
4	112	FD	0.641	533.0464	0	768.358	0
4	113	D	0.962	332.7144	0	657.987	0
4	113	F	0.51	137.7204	0	319.25165	0
4	113	C	1.243	167.99	0	196.94865	0
4	113	FD	0.471	214.03025	0	290.64625	0
4	104	D	0.844	748.78795	0	775.93325	0
4	104	F	1.243	170.816	0	301.283	0
4	104	C	1.158	346.2164	0	949.29265	0
4	104	FD	0.589	377.6164	0	487.99525	0
4	105	F	1.272	307.7514	0	556.094	0
4	105	D	1.102	345.5884	0	728.6684	0
4	105	C	1.328	0	1	0	1
4	105	FD	1.3	529.2784	0	889.0753	0
4	109	FD	1.354	189.813	0	310.232	0
4	109	D	1.138	0	1	25.277	0
4	109	F	1.413	248.531	0	391.4324	0
4	109	C	0.276	22.49025	0	0	1
4	111	C	0.491	142.242	0	191.7284	0
4	111	FD	2.063	395.012	0	802.02665	0
4	111	F	1.629	350.1414	0	675.7594	0
4	111	D	1.272	0	1	0	1
4	124	F	0.471	121.8634	0	470.058	0
4	124	D	1.295	148.993	0	431.279	0
4	124	C	3.297	131.88	0	397.367	0
4	124	FD	3.808	636.0384	0	1028.35	0
4	123	D	1.06	453.4474	0	1035.7682	0
4	123	FD	0.412	45.53	0	122.46	0
4	123	F	1.119	413.2868	0	547.30985	0
4	123	C	0.275	164.536	0	374.04465	0
4	130	F	0.44	312.901	0	551.384	0
4	130	D	1.187	217.916	0	60.602	0
4	130	C	0.509	122.46	0	214.148	0
4	130	FD	0.961	0	1	0	1
4	129	D	0.424	182.81865	0	300.341	0
4	129	F	0.553	191.697	0	330.956	0
4	129	C	1.187	307.877	0	443.56425	0
4	129	FD	1.001	384.9954	0	898.982	0
4	107	D	0.628	148.679	0	302.225	0
4	107	FD	1.809	0	1	0	1
4	107	C	1.079	273.18	0	366.909	0
4	107	F	1.102	277.89	0	210.26225	0
4	110	D	0.48	0	1	0	1
4	110	F	2.154	229.848	0	393.32425	0
4	110	C	1.102	241.81925	0	274.593	0
4	110	FD	0.452	104.405	0	227.84625	0
4	106	F	1.243	292.3654	0	585.767	0
4	106	D	0.236	92.54365	0	177.76325	0

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
4	106	C	0.864	182.1514	0	135.68725	0
4	106	FD	0.903	259.24625	0	784.12865	0
4	108	F	0.412	83.995	0	187.929	0
4	108	C	0.412	75.08525	0	197.4118	0
4	108	FD	0.314	17.27	0	0	1
4	108	D	1.017	232.08525	0	411.497	0
4	114	C	0.82	0	1	0	1
4	114	FD	0.707	218.387	0	0	1
4	114	F	0.844	146.324	0	190.29185	0
4	114	D	1.328	329.8884	0	520.46285	0
4	115	F	2.154	356.93165	0	681.223	0
4	115	C	0.339	121.7064	0	170.816	0
4	115	FD	0.414	104.405	0	218.858	0
4	115	D	0.569	237.7294	0	449.2241	0
4	119	D	1.159	464.31965	0	0	1
4	119	C	1.335	244.292	0	124.815	0
4	119	FD	0.301	215.09	0	1090.5612	0
4	119	F	1.724	271.296	0	341.0354	0
4	118	C	0.785	420.0064	0	435.047	0
4	118	D	0.49	214.148	0	96.12325	0
4	118	F	1.217	351.27965	0	529.28625	0
4	118	FD	1.78	547.4904	0	1155.7555	0
4	128	FD	0.373	63.428	0	167.99	0
4	128	C	0.471	239.1424	0	471.942	0
4	128	F	0.569	194.523	0	433.163	0
4	128	D	1.809	586.7404	0	1228.368	0
4	126	F	0.765	496.1514	0	462.836	0
4	126	FD	0.254	111.156	0	215.09	0
4	126	D	1.335	444.3414	0	556.094	0
4	126	C	0.765	341.3494	0	0	1
5	177	FD	0.791	112.16865	0	0	1
5	177	F	0.393	156.0894	0	172.7	0
5	177	C	1.356	117.47525	0	284.20925	0
5	177	D	0.824	571.6684	0	435.71425	0
5	171	C	0.352	418.1224	0	431.75	0
5	171	FD	0.846	319.09465	0	258.736	0
5	171	F	0.353	125.757	0	42.58625	0
5	171	D	1.507	303.0414	0	616.382	0
5	191	C	0.51	172.7	0	166.577	0
5	191	FD	3.923	944.7318	0	556.3609	0
5	191	F	0.502	400.664	0	520.769	0
5	191	D	0.666	273.18	0	517.001	0
5	190	D	0.687	216.503	0	62.486	0
5	190	F	0.603	521.083	0	23.6756	0
5	190	C	0.962	191.226	0	351.9155	0
5	190	FD	1.328	472.1304	0	216.032	0
5	175	F	0.432	206.0154	0	532.11225	0
5	175	D	0.735	240.053	0	521.711	0
5	175	C	1.046	122.8054	0	72.063	0
5	175	FD	0.678	340.2504	0	661.598	0
5	199	F	0.876	497.219	0	0	1
5	199	FD	1.356	435.518	0	802.427	0
5	199	C	1.472	285.583	0	648.4885	0
5	199	D	1	304.109	0	0	1
5	194	F	0.904	565.6239	0	72.10225	0
5	194	C	2.539	204.17065	0	583.51405	0
5	194	FD	1	273.18	0	0	1
5	194	D	0.785	331.898	0	0	1

SITE	BLOCK	TREAT	RVOLUME	BIOMASS00	RDEATH00	BIOMASS01	RDEATH01
5	198	C	0.962	321.4104	0	459.225	0
5	198	FD	1.923	414.3544	0	936.976	0
5	198	D	0.687	188.871	0	188.871	0
5	198	F	1.539	474.0144	0	341.475	0
5	180	D	0.933	47.0215	0	511.07425	0
5	180	C	1.893	613.78365	0	1057.709	0
5	180	F	1.554	614.69425	0	735.074	0
5	180	FD	0.962	332.84	0	0	1
5	181	D	0.565	280.78665	0	0	1
5	181	FD	1.328	305.051	0	527.363	0
5	181	F	1.215	466.0074	0	700.0159	0
5	181	C	0.55	0	1	0	1
5	197	FD	0.451	123.402	0	0	1
5	197	C	1.328	175.40825	0	0	1
5	197	D	0.402	282.79625	0	0	1
5	197	F	0.791	299.75225	0	130.781	0
5	178	F	0.48	142.94065	0	243.821	0
5	178	FD	1.47	0	1	0	1
5	178	D	0.844	233.65525	0	459.29565	0
5	178	C	0.339	148.24725	0	80.73725	0
5	174	FD	0.276	0	1	0	1
5	174	D	0.883	352.53565	0	0	1
5	174	F	2.864	421.4665	0	0	1
5	174	C	0.707	446.3824	0	269.883	0
5	185	D	0.667	175.84	0	0	1
5	185	C	0.763	75.87025	0	0	1
5	185	FD	1.356	128.112	0	0	1
5	185	F	1.23	110.371	0	0	1
5	189	C	0.569	649.2264	0	865.42325	0
5	189	D	0.412	162.25165	0	12.252	0
5	189	F	1.13	226.90425	0	290.921	0
5	189	FD	1.385	0	1	0	1
5	195	D	0.412	0	1	0	1
5	195	FD	0.687	420.446	0	80.855	0
5	195	F	0.327	0	1	0	1
5	195	C	0.251	0	1	0	1
5	183	F	1.159	193.581	0	435.518	0
5	183	FD	0.402	215.561	0	545.418	0
5	183	C	1.385	0	1	0	1
5	183	D	1.608	31.28225	0	38.936	0
5	179	D	2.798	835.93865	0	1023.9932	0
5	179	C	0.276	53.73325	0	57.776	0
5	179	F	0.989	196.7995	0	389.93305	0
5	179	FD	0.726	0	1	0	1
5	176	F	0.933	273.9964	0	512.291	0
5	176	FD	0.82	419.07225	0	944.512	0
5	176	C	0.515	124.344	0	269.412	0
5	176	D	0.389	346.85225	0	1071.2502	0
5	186	FD	1.577	771.72565	0	629.57	0
5	186	D	0.49	444.3414	0	687.503	0
5	186	F	0.824	250.415	0	232.05385	0
5	186	C	0.412	532.1044	0	354.38825	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
1	161	C	9.1	2	1	1	0	0	0	0
1	161	FD	9.1	1	1	1	1	0	0	0
1	161	D	9.1	2	2	2	2	0	0	0
1	161	F	9.1	2	2	1	1	0	0	0
1	150	D	7.1	3	2	0	0	0	0	0
1	150	C	7.1	0	0	0	0	0	0	0
1	150	FD	7.1	1	1	0	0	0	0	0
1	150	F	7.1	1	1	0	0	0	0	0
1	142	D	9.3	1	0	0	0	0	0	0
1	142	C	9.3	2	3	0	0	0	0	0
1	142	F	9.3	0	0	0	0	0	0	0
1	142	FD	9.3	2	2	1	1	0	0	0
1	143	D	7.5	1	2	1	1	0	0	0
1	143	FD	7.5	1	0	1	1	0	0	0
1	143	F	7.5	1	1	1	0	0	0	0
1	143	C	7.5	1	0	0	0	0	0	0
1	149	C	11.1	0	0	0	0	0	0	0
1	149	F	11.1	1	0	1	0	0	0	0
1	149	D	11.1	1	3	1	1	0	0	0
1	149	FD	11.1	1	1	1	0	0	0	0
1	144	FD	9.5	2	1	1	1	14	1	1
1	144	C	9.5	1	2	1	1	0	0	0
1	144	F	9.5	1	1	0	0	0	0	0
1	144	D	9.5	1	1	0	0	0	1	0
1	146	FD	8.7	2	2	0	0	0	0	0
1	146	C	8.7	2	2	1	1	0	0	0
1	146	D	8.7	3	0	0	0	0	0	0
1	146	F	8.7	1	0	1	0	0	0	0
1	141	FD	7.3	1	0	1	0	0	0	0
1	141	F	7.3	1	1	0	0	0	1	1
1	141	C	7.3	1	1	0	0	0	0	0
1	141	D	7.3	3	3	3	0	0	0	0
1	162	D	8.1	1	0	1	1	0	0	0
1	162	C	8.1	1	0	0	0	0	0	0
1	162	FD	8.1	1	0	0	0	0	0	0
1	162	F	8.1	1	1	0	0	0	0	0
1	166	C	6.1	1	1	0	0	0	1	0
1	166	FD	6.1	1	0	1	1	0	0	0
1	166	F	6.1	0	0	0	0	0	0	0
1	166	D	6.1	0	0	0	0	0	0	0
1	160	D	7.3	1	2	1	1	0	0	0
1	160	F	7.3	2	0	1	1	0	0	0
1	160	FD	7.3	2	0	1	1	0	0	0
1	160	C	7.3	0	0	0	0	0	0	0
1	158	C	4.7	2	1	0	1	0	0	0
1	158	F	4.7	1	1	1	0	0	0	0
1	158	D	4.7	1	1	0	1	0	1	0
1	158	FD	4.7	1	0	1	0	0	0	0
1	151	F	8.8	1	0	1	0	0	0	0
1	151	C	8.8	2	3	1	1	0	1	0
1	151	FD	8.8	1	0	0	0	0	0	0
1	151	D	8.8	1	1	1	1	0	1	0
1	154	FD	9.6	1	1	0	0	15	1	1
1	154	F	9.6	1	0	1	0	0	0	0
1	154	D	9.6	3	2	2	1	0	0	0
1	154	C	9.6	2	1	1	0	0	0	0
1	153	FD	8.6	1	1	0	0	0	0	0
1	153	D	8.6	1	0	0	0	0	0	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
1	153	F	8.6	1	2	1	0	0	0	0
1	153	C	8.6	1	0	0	0	0	0	0
1	159	D	8	1	0	1	1	0	0	0
1	159	F	8	1	0	0	0	0	0	0
1	159	C	8	3	0	0	0	0	0	0
1	159	FD	8	1	2	0	1	0	0	0
1	167	F	8.8	1	0	0	0	0	0	0
1	167	FD	8.8	2	0	2	2	0	0	0
1	167	C	8.8	1	2	1	1	0	0	0
1	167	D	8.8	1	2	0	0	0	0	0
1	168	D	8.7	1	2	1	1	0	0	0
1	168	FD	8.7	2	1	1	1	0	0	0
1	168	F	8.7	3	1	1	1	14	1	1
1	168	C	8.7	1	1	1	1	0	0	0
1	169	C	6.7	1	3	0	0	0	1	0
1	169	F	6.7	1	1	1	1	8	1	1
1	169	FD	6.7	2	1	0	0	10	1	1
1	169	D	6.7	2	1	2	2	0	0	0
1	145	FD	6.6	0	0	0	0	0	0	0
1	145	F	6.6	1	1	1	1	0	0	0
1	145	D	6.6	1	2	1	1	0	1	0
1	145	C	6.6	1	1	0	0	0	1	0
2	59	FD	5	1	1	1	1	0	0	0
2	59	F	5	1	0	0	0	0	0	0
2	59	C	5	2	0	0	0	0	0	0
2	59	D	5	0	0	0	0	0	0	0
2	60	F	6.6	2	1	1	1	0	0	0
2	60	D	6.6	1	1	1	1	9	1	1
2	60	FD	6.6	2	1	0	0	0	0	0
2	60	C	6.6	1	0	0	0	0	0	0
2	61	D	7.5	1	1	0	0	0	0	0
2	61	FD	7.5	1	1	1	1	0	0	0
2	61	F	7.5	1	0	0	0	0	0	0
2	61	C	7.5	1	0	0	0	0	0	0
2	62	FD	6.8	1	0	0	0	0	0	0
2	62	F	6.8	1	1	1	1	0	0	0
2	62	C	6.8	1	0	0	0	0	0	0
2	62	D	6.8	1	0	0	0	0	0	0
2	64	C	5.2	1	1	0	0	0	0	0
2	64	FD	5.2	1	1	0	0	0	0	0
2	64	D	5.2	1	1	0	0	11	1	1
2	64	F	5.2	1	1	1	1	0	0	0
2	65	D	8.7	1	1	0	0	0	0	0
2	65	F	8.7	1	0	1	1	0	0	0
2	65	C	8.7	1	0	1	0	0	0	0
2	65	FD	8.7	1	1	0	0	12	1	1
2	67	F	8.5	1	1	1	1	0	0	0
2	67	C	8.5	0	0	0	0	0	0	0
2	67	D	8.5	0	0	0	0	0	0	0
2	67	FD	8.5	1	0	0	0	0	0	0
2	66	F	7.8	1	1	0	0	0	0	0
2	66	D	7.8	1	1	0	0	0	0	0
2	66	C	7.8	1	1	1	1	0	0	0
2	66	FD	7.8	1	1	1	0	9	1	1
2	63	FD	5.7	2	1	0	0	0	0	0
2	63	D	5.7	1	0	0	0	0	0	0
2	63	C	5.7	1	1	1	1	0	0	0
2	63	F	5.7	1	1	1	1	0	0	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
2	70	C	8.7	1	1	1	1	0	0	0
2	70	D	8.7	1	1	1	1	12	1	1
2	70	F	8.7	2	0	1	0	0	0	0
2	70	FD	8.7	1	1	0	0	13	1	1
2	69	D	8.5	1	0	0	0	0	0	0
2	69	F	8.5	0	0	0	0	0	0	0
2	69	FD	8.5	0	0	0	0	0	0	0
2	69	C	8.5	0	0	0	0	0	0	0
2	68	C	7.7	1	1	1	1	0	0	0
2	68	D	7.7	0	0	0	0	0	0	0
2	68	FD	7.7	1	0	0	0	0	0	0
2	68	F	7.7	0	0	0	0	0	0	0
2	71	FD	7.4	1	1	0	0	0	0	0
2	71	C	7.4	0	0	0	0	0	0	0
2	71	F	7.4	2	1	0	0	7	1	1
2	71	D	7.4	1	0	1	1	0	1	0
2	72	D	10	1	1	0	0	0	0	0
2	72	F	10	0	0	0	0	0	0	0
2	72	C	10	0	0	0	0	0	0	0
2	72	FD	10	1	1	0	0	0	0	0
2	73	F	14.2	0	0	0	0	0	0	0
2	73	FD	14.2	1	1	0	0	0	0	0
2	73	D	14.2	2	2	0	0	0	0	0
2	73	C	14.2	0	0	0	0	0	0	0
2	74	F	7.7	1	1	0	0	0	0	0
2	74	FD	7.7	2	1	0	0	0	0	0
2	74	D	7.7	1	0	0	0	0	0	0
2	74	C	7.7	1	1	0	0	0	0	0
2	77	C	8.8	2	2	2	2	21	1	1
2	77	FD	8.8	1	0	0	0	0	0	0
2	77	F	8.8	0	0	0	0	0	0	0
2	77	D	8.8	1	1	0	0	0	0	0
2	78	FD	6.9	2	1	0	0	0	0	0
2	78	F	6.9	2	0	0	0	0	0	0
2	78	C	6.9	1	1	0	0	0	0	0
2	78	D	6.9	1	0	0	0	0	0	0
2	79	D	8.4	0	0	0	0	0	0	0
2	79	F	8.4	0	0	0	0	0	0	0
2	79	C	8.4	1	1	0	0	0	0	0
2	79	FD	8.4	1	1	0	0	0	0	0
2	80	FD	9	3	2	0	0	0	0	0
2	80	C	9	1	0	0	0	0	0	0
2	80	F	9	1	0	0	0	0	0	0
2	80	D	9	1	2	0	0	0	0	0
3	138	D	31	1	1	1	1	0	0	0
3	138	C	31	1	1	0	0	0	0	0
3	138	F	31	2	2	0	0	0	0	0
3	138	FD	31	2	1	1	0	0	0	0
3	98	FD	16.8	2	2	0	0	8	1	1
3	98	C	16.8	3	1	1	0	0	0	0
3	98	F	16.8	2	0	0	0	0	0	0
3	98	D	16.8	3	2	1	0	0	0	0
3	133	C	18.2	1	2	0	0	0	0	0
3	133	F	18.2	4	1	0	0	4	1	1
3	133	D	18.2	1	1	1	1	15	1	1
3	133	FD	18.2	1	1	1	1	17	1	1
3	132	FD	21.2	1	1	1	1	13	1	1
3	132	C	21.2	1	0	1	1	0	0	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
3	132	D	21.2	1	1	1	1	14	1	1
3	132	F	21.2	2	1	0	0	0	1	0
3	131	D	12.9	1	1	1	1	8	1	1
3	131	FD	12.9	2	1	0	0	0	0	0
3	131	F	12.9	0	0	0	0	0	0	0
3	131	C	12.9	1	1	1	1	12	1	1
3	91	FD	34.2	0	0	0	0	0	0	0
3	91	C	34.2	0	0	0	0	0	0	0
3	91	F	34.2	0	0	0	0	0	0	0
3	91	D	34.2	0	0	0	0	0	0	0
3	86	FD	37	3	1	0	0	0	1	0
3	86	D	37	0	0	0	0	0	0	0
3	86	C	37	0	0	0	0	0	0	0
3	86	F	37	0	0	0	0	0	0	0
3	99	C		2	2	0	0	0		0
3	99	F		3	3	0	0	0		0
3	99	D		1	0	0	0	0		
3	99	FD		0	0	0	0	0		
3	100	FD		0		0	0			
3	100	F		0		0	0			
3	100	D		1		1	0			
3	100	C		0		0	0			
3	96	FD	12.9	2	1	1	1	0	0	0
3	96	F	12.9	1	1	0	0	8	1	1
3	96	D	12.9	5	3	0	0	0	0	0
3	96	C	12.9	1	1	1	0	0	0	0
3	81	F	50.5	1	1	0	0	0	0	0
3	81	C	50.5	1	1	0	0	0	0	0
3	81	FD	50.5	0	0	0	0	0	0	0
3	81	D	50.5	0	0	0	0	0	0	0
3	94	FD	14.1	2	1	0	0	0	0	0
3	94	D	14.1	4	2	0	0	0	0	0
3	94	F	14.1	1	2	1	1	0	0	0
3	94	C	14.1	1	1	0	0	0	0	0
3	82	C	33.6	1	1	0	0	0	0	0
3	82	F	33.6	1	0	1	1	0	0	0
3	82	FD	33.6	3	0	0	0	0	0	0
3	82	D	33.6	2	1	0	0	0	0	0
3	90	F	22.9	0	0	0	0	0	0	0
3	90	D	22.9	2	1	0	0	0	0	0
3	90	C	22.9	0	0	0	0	0	0	0
3	90	FD	22.9	1	1	1	1	9	1	1
3	137	D	21.4	1	1	0	0	8	1	1
3	137	FD	21.4	1	1	0	0	0	0	0
3	137	F	21.4	1	1	1	1	20	1	1
3	137	C	21.4	1	1	1	1	11	1	1
3	88	F	21.9	3	1	0	0	0	0	0
3	88	D	21.9	3	3	1	1	8	1	1
3	88	FD	21.9	2	1	0	0	7	1	1
3	88	C	21.9	1	1	1	0	0	0	0
3	89	C	37.9	1	1	0	0	0	1	0
3	89	D	37.9	0	0	0	0	0	0	0
3	89	FD	37.9	1	1	1	1	6	1	1
3	89	F	37.9	3	2	0	0	0	1	0
3	87	F	36.3	0	0	0	0	0	0	0
3	87	D	36.3	1	1	1	1	7	1	1
3	87	C	36.3	2	1	0	0	0	0	0
3	87	FD	36.3	0	0	0	0	0	0	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
3	95	C	15	2	2	0	0	11	1	1
3	95	F	15	1	2	1	0	0	0	0
3	95	D	15	0	0	0	0	0	0	0
3	95	FD	15	0	0	0	0	0	0	0
3	97	FD	35.3	2	1	0	0	0	0	0
3	97	C	35.3	3	0	0	0	0	0	0
3	97	F	35.3	3	0	0	0	0	0	0
3	97	D	35.3	3	1	0	0	0	0	0
4	112	D	18.8	1	1	0	0	0	0	0
4	112	C	18.8	1	1	0	0	0	0	0
4	112	F	18.8	1	1	1	1	0	0	0
4	112	FD	18.8	2	2	1	1	0	0	0
4	113	D	20.2	1	1	1	1	9	1	1
4	113	F	20.2	1	1	1	1	0	0	0
4	113	C	20.2	1	1	0	0	0	0	0
4	113	FD	20.2	2	2	0	0	0	0	0
4	104	D	13.8	4	1	3	3	13	1	1
4	104	F	13.8	1	1	0	0	0	0	0
4	104	C	13.8	2	1	1	1	0	0	0
4	104	FD	13.8	1	2	1	1	0	1	0
4	105	F	17.6	1	1	1	1	0	0	0
4	105	D	17.6	2	1	1	1	13	1	1
4	105	C	17.6	0	0	0	0	0	0	0
4	105	FD	17.6	1	2	1	1	14	1	1
4	109	FD	7.6	1	1	0	0	10	1	1
4	109	D	7.6	0	1	0	0	0	0	0
4	109	F	7.6	2	1	1	0	0	0	0
4	109	C	7.6	1	0	0	0	0	0	0
4	111	C	24.1	2	1	0	0	0	0	0
4	111	FD	24.1	2	2	0	0	0	0	0
4	111	F	24.1	1	1	0	1	11	1	1
4	111	D	24.1	0	0	0	0	0	0	0
4	124	F	16.4	1	1	1	1	0	0	0
4	124	D	16.4	2	1	0	0	0	0	0
4	124	C	16.4	1	1	0	0	0	0	0
4	124	FD	16.4	1	1	1	1	21	1	1
4	123	D	21.9	1	2	1	1	0	1	0
4	123	FD	21.9	1	1	0	0	0	0	0
4	123	F	21.9	1	1	1	1	0	0	0
4	123	C	21.9	1	1	1	0	0	0	0
4	130	F	24.3	2	1	0	0	0	0	0
4	130	D	24.3	1	1	0	0	0	0	0
4	130	C	24.3	1	1	0	0	0	0	0
4	130	FD	24.3	0	0	0	0	0	0	0
4	129	D	14.3	1	1	1	1	0	0	0
4	129	F	14.3	1	1	0	0	0	0	0
4	129	C	14.3	1	1	0	0	15	1	1
4	129	FD	14.3	1	1	1	1	11	1	1
4	107	D	12.3	1	1	0	0	0	0	0
4	107	FD	12.3	0	0	0	0	0	0	0
4	107	C	12.3	1	1	0	0	0	1	0
4	107	F	12.3	1	1	0	0	0	0	0
4	110	D	11.5	0	0	0	0	0	0	0
4	110	F	11.5	1	1	1	0	10	1	1
4	110	C	11.5	2	1	1	0	0	0	0
4	110	FD	11.5	1	1	0	0	0	0	0
4	106	F	9.7	1	1	1	1	9	1	1
4	106	D	9.7	1	1	1	1	0	0	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
4	106	C	9.7	1	3	1	1	0	0	0
4	106	FD	9.7	1	3	0	0	12	1	1
4	108	F	14	2	1	0	0	0	0	0
4	108	C	14	2	2	0	0	0	0	0
4	108	FD	14	1	0	0	0	0	0	0
4	108	D	14	2	1	1	0	12	1	1
4	114	C	25	0	0	0	0	0	0	0
4	114	FD	25	1	0	0	0	0	0	0
4	114	F	25	2	1	0	0	0	0	0
4	114	D	25	1	1	1	1	15	1	1
4	115	F	16.2	1	2	1	1	9	1	1
4	115	C	16.2	1	1	1	1	0	0	0
4	115	FD	16.2	1	1	0	0	0	0	0
4	115	D	16.2	1	1	1	1	7	1	1
4	119	D	29.6	2	0	0	1	0	0	0
4	119	C	29.6	1	1	0	0	0	0	0
4	119	FD	29.6	1	2	0	0	0	0	0
4	119	F	29.6	1	1	0	0	0	0	0
4	118	C	24.3	1	1	1	1	0	0	0
4	118	D	24.3	1	2	0	0	0	0	0
4	118	F	24.3	1	1	1	1	0	0	0
4	118	FD	24.3	1	2	1	1	13	1	1
4	128	FD	17.5	1	1	0	0	0	0	0
4	128	C	17.5	1	1	1	1	0	0	0
4	128	F	17.5	1	1	0	0	0	0	0
4	128	D	17.5	1	2	1	1	16	1	1
4	126	F	10.1	1	2	1	1	0	0	0
4	126	FD	10.1	1	1	1	0	0	0	0
4	126	D	10.1	1	1	1	1	0	0	0
4	126	C	10.1	1	0	1	1	0	0	0
5	177	FD	5.2	1	0	1	0	0	0	0
5	177	F	5.2	3	1	1	0	0	0	0
5	177	C	5.2	1	1	0	0	0	0	0
5	177	D	5.2	1	1	1	1	0	1	0
5	171	C	6.9	1	1	1	1	0	0	0
5	171	FD	6.9	1	2	1	1	0	0	0
5	171	F	6.9	1	1	0	0	0	0	0
5	171	D	6.9	1	1	1	1	0	0	0
5	191	C	7.9	1	1	0	0	0	0	0
5	191	FD	7.9	2	2	2	2	8	2	1
5	191	F	7.9	1	1	0	0	0	0	0
5	191	D	7.9	1	1	0	0	0	0	0
5	190	D	9.2	1	1	0	0	0	0	0
5	190	F	9.2	2	1	0	0	0	0	0
5	190	C	9.2	1	3	0	0	0	0	0
5	190	FD	9.2	1	1	1	1	0	0	0
5	175	F	6.8	1	1	1	1	0	0	0
5	175	D	6.8	1	2	0	0	0	0	0
5	175	C	6.8	1	1	0	1	0	0	0
5	175	FD	6.8	1	1	1	1	9	1	1
5	199	F	5.4	3	0	0	0	0	0	0
5	199	FD	5.4	1	2	0	0	0	0	0
5	199	C	5.4	1	5	1	0	0	0	0
5	199	D	5.4	1	0	0	0	0	0	0
5	194	F	7.2	2	2	1	1	0	0	0
5	194	C	7.2	3	3	1	1	0	0	0
5	194	FD	7.2	1	0	0	0	0	0	0
5	194	D	7.2	1	0	0	1	0	0	0

SITE	BLOCK	TREAT	PAR	STEMS00	STEMS01	FLOWER00	FRUIT00	TSEEDS	FLOWER01	FRUIT01
5	198	C	5.9	1	2	1	1	0	0	0
5	198	FD	5.9	1	1	0	1	0	1	0
5	198	D	5.9	1	1	1	0	0	0	0
5	198	F	5.9	1	0	1	1	0	1	0
5	180	D	5.5	1	2	1	0	0	0	0
5	180	C	5.5	5	4	1	1	0	1	0
5	180	F	5.5	3	2	0	0	0	0	0
5	180	FD	5.5	1	0	0	0	0	0	0
5	181	D	5.1	1	0	1	1	0	0	0
5	181	FD	5.1	1	1	0	0	9	1	1
5	181	F	5.1	2	2	1	1	0	0	0
5	181	C	5.1	0	0	0	0	0	0	0
5	197	FD	6.5	1	0	0	0	0	0	0
5	197	C	6.5	1	0	0	0	0	0	0
5	197	D	6.5	1	0	0	0	0	0	0
5	197	F	6.5	2	2	0	0	0	0	0
5	178	F	7.2	1	1	1	1	0	0	0
5	178	FD	7.2	0	0	0	0	0	0	0
5	178	D	7.2	3	3	0	0	0	0	0
5	178	C	7.2	3	1	0	0	0	0	0
5	174	FD	8.4	0	0	0	0	0	0	0
5	174	D	8.4	2	0	1	1	0	0	0
5	174	F	8.4	1	0	1	0	0	0	0
5	174	C	8.4	1	1	1	1	0	0	0
5	185	D	5.8	1	0	1	0	0	0	0
5	185	C	5.8	1	0	1	0	0	0	0
5	185	FD	5.8	1	0	0	0	0	0	0
5	185	F	5.8	1	0	1	0	0	0	0
5	189	C	11.5	2	1	1	1	6	1	1
5	189	D	11.5	1	1	0	1	0	0	0
5	189	F	11.5	1	2	0	0	0	0	0
5	189	FD	11.5	0	0	0	0	0	0	0
5	195	D	5	0	0	0	0	0	0	0
5	195	FD	5	2	2	0	0	0	0	0
5	195	F	5	0	0	0	0	0	0	0
5	195	C	5	0	0	0	0	0	0	0
5	183	F	6.7	1	1	0	0	0	0	0
5	183	FD	6.7	1	1	0	0	7	1	1
5	183	C	6.7	0	0	0	0	0	0	0
5	183	D	6.7	1	1	0	0	0	0	0
5	179	D	8.2	2	1	1	1	0	1	0
5	179	C	8.2	2	1	0	0	0	0	0
5	179	F	8.2	2	2	0	0	0	0	0
5	179	FD	8.2	0	0	0	0	0	0	0
5	176	F	5.3	1	1	1	1	0	0	0
5	176	FD	5.3	1	1	0	0	0	1	0
5	176	C	5.3	1	1	0	0	0	0	0
5	176	D	5.3	1	1	0	0	0	0	0
5	186	FD	8.1	1	4	1	1	0	1	0
5	186	D	8.1	1	1	1	1	0	1	0
5	186	F	8.1	1	1	0	0	0	0	0
5	186	C	8.1	1	4	1	1	0	0	0

Appendix F

Seed Data from Experiment

Variables:

SITE
BLOCK
TREAT
PAR = photosynthetically active radiation, $\mu E/cm^2 sec$
SDLGS = seedlings
GERM = occurrence of germination (1 = yes, 0 = no)

SITE	BLOCK	TREAT	PAR	SDLGS	GERM		SITE	BLOCK	TREAT	PAR	SDLGS	GERM
1	147	C	9.2	0	0		2	51	C	6.6	4	1
1	147	F	9.2	0	0		2	51	F	6.6	1	1
1	147	FD	9.2	0	0		2	51	FD	6.6	0	0
1	147	D	9.2	0	0		2	51	D	6.6	0	0
1	148	C	9.9	0	0		2	52	C	6.7	0	0
1	148	F	9.9	0	0		2	52	F	6.7	0	0
1	148	FD	9.9	0	0		2	52	FD	6.7	0	0
1	148	D	9.9	0	0		2	52	D	6.7	0	0
1	152	C	8.7	0	0		2	53	C	5.9	3	1
1	152	F	8.7	0	0		2	53	F	5.9	1	1
1	152	FD	8.7	0	0		2	53	FD	5.9	0	0
1	152	D	8.7	0	0		2	53	D	5.9	1	1
1	155	C	7.2	0	0		2	54	C	6.6	4	1
1	155	F	7.2	0	0		2	54	F	6.6	0	0
1	155	FD	7.2	0	0		2	54	FD	6.6	1	1
1	155	D	7.2	0	0		2	54	D	6.6	0	0
1	156	C	5.1	0	0		2	55	C	8.4	5	1
1	156	F	5.1	0	0		2	55	F	8.4	0	0
1	156	FD	5.1	0	0		2	55	FD	8.4	0	0
1	156	D	5.1	0	0		2	55	D	8.4	0	0
1	157	C	4.7	0	0		2	56	C	5.2	0	0
1	157	F	4.7	0	0		2	56	F	5.2	6	1
1	157	FD	4.7	0	0		2	56	FD	5.2	1	1
1	157	D	4.7	0	0		2	56	D	5.2	3	1
1	163	C	7.1	0	0		2	57	C	5.3	0	0
1	163	F	7.1	0	0		2	57	F	5.3	0	0
1	163	FD	7.1	0	0		2	57	FD	5.3	0	0
1	163	D	7.1	0	0		2	57	D	5.3	1	1
1	164	C	8.5	0	0		2	58	C	6.1	0	0
1	164	F	8.5	0	0		2	58	F	6.1	0	0
1	164	FD	8.5	0	0		2	58	FD	6.1	0	0
1	164	D	8.5	2	1		2	58	D	6.1	0	0
1	165	C	4.9	0	0		2	75	C	9.8	1	1
1	165	F	4.9	0	0		2	75	F	9.8	0	0
1	165	FD	4.9	0	0		2	75	FD	9.8	0	0
1	165	D	4.9	0	0		2	75	D	9.8	0	0
1	170	C	6.5	0	0		2	76	C	6.9	0	0
1	170	F	6.5	0	0		2	76	F	6.9	0	0
1	170	FD	6.5	0	0		2	76	FD	6.9	0	0
1	170	D	6.5	0	0		2	76	D	6.9	0	0

TREAT = treatment; C = control, F = fertlized, D = soil turnover, FD = fertilized + soil turnover

PAR = photosynthetically active radiation (u E/cm-squaredsec)

SDLGS = # seedlings

GERM = occurrence of germination (0 = no, 1 = yes)

SITE	BLOCK	TREAT	PAR	SDLGS	GERM		SITE	BLOCK	TREAT	PAR	SDLGS	GERM
3	134	C	13.7	4	1		4	101	C	12.7	0	0
3	134	F	13.7	0	0		4	101	F	12.7	1	1
3	134	FD	13.7	0	0		4	101	FD	12.7	0	0
3	134	D	13.7	0	0		4	101	D	12.7	0	0
3	135	C	16	0	0		4	102	C	15.3	0	0
3	135	F	16	0	0		4	102	F	15.3	1	1
3	135	FD	16	0	0		4	102	FD	15.3	1	1
3	135	D	16	3	1		4	102	D	15.3	1	1
3	136	C	20.1	2	1		4	103	C	13.2	0	0
3	136	F	20.1	3	1		4	103	F	13.2	0	0
3	136	FD	20.1	1	1		4	103	FD	13.2	0	0
3	136	D	20.1	2	1		4	103	D	13.2	1	1
3	139	C	18.5	1	1		4	116	C	10.4	1	1
3	139	F	18.5	0	0		4	116	F	10.4	0	0
3	139	FD	18.5	1	1		4	116	FD	10.4	0	0
3	139	D	18.5	0	0		4	116	D	10.4	0	0
3	140	C	22.5	3	1		4	117	C	10.4	0	0
3	140	F	22.5	0	0		4	117	F	10.4	0	0
3	140	FD	22.5	0	0		4	117	FD	10.4	0	0
3	140	D	22.5	0	0		4	117	D	10.4	0	0
3	83	C	13.9	1	1		4	120	C	10.3	0	0
3	83	F	13.9	6	1		4	120	F	10.3	1	1
3	83	FD	13.9	2	1		4	120	FD	10.3	1	1
3	83	D	13.9	3	1		4	120	D	10.3	1	1
3	84	C	15.4	3	1		4	121	C	16.3	1	1
3	84	F	15.4	8	1		4	121	F	16.3	1	1
3	84	FD	15.4	6	1		4	121	FD	16.3	0	0
3	84	D	15.4	2	1		4	121	D	16.3	0	0
3	85	C	19.8	5	1		4	122	C	21	1	1
3	85	F	19.8	6	1		4	122	F	21	0	0
3	85	FD	19.8	3	1		4	122	FD	21	0	0
3	85	D	19.8	8	1		4	122	D	21	0	0
3	92	C	29.5	0	0		4	125	C	17.7	0	0
3	92	F	29.5	0	0		4	125	F	17.7	0	0
3	92	FD	29.5	6	1		4	125	FD	17.7	1	1
3	92	D	29.5	4	1		4	125	D	17.7	0	0
3	93	C	11.3	0	0		4	127	C	34.2	0	0
3	93	F	11.3	0	0		4	127	F	34.2	0	0
3	93	FD	11.3	0	0		4	127	FD	34.2	2	1
3	93	D	11.3	0	0		4	127	D	34.2	2	1

TREAT = treatment: C = control, F = fertlized, D = soil turnover, FD = fertilized + soil turnover

PAR = photosynthetically active radiation (*u* E/cm-squaredsec)

SDLGS = # seedlings

GERM = occurrence of germination (0 = no, 1 = yes)