ABSTRACT

Title of Dissertation:  DISTURBANCE BY FIRE AND ITS ROLE IN THE POPULATION BIOLOGY AND DISTRIBUTION OF A RARE TEMPERATE FOREST HERB

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This research comprises a comprehensive investigation of the role and effects of disturbance by fire on the population biology of turkeybeard (*Xerophyllum asphodeloides*: Melanthiaceae) a rare forest herb of the Appalachian Mountains. I first employ a long term monitoring dataset from a primary study population to examine demography and flowering patterns. The effects of forest disturbance on survival, fruit and seed production in this population are next investigated by evaluating the outcome of a controlled, fire and canopy alteration 'pulse' experiment. The pollination biology of *X. asphodeloides* in the context of the above habitat manipulation is then determined from hand pollination experiments over three flowering seasons. Lastly, the role of fire and other environmental variables in the distribution of *X. asphodeloides* populations at the landscape scale is assessed via the construction, cross-validation, and ground-truthing of a classification tree and geographic information system (GIS)–based predictive habitat model for the mountains of northwestern Virginia, U.S.A.

The major results demonstrate that *X. asphodeloides* is one of the few definitively fire-adapted forest understory herbs in the eastern United States. This is due to a number of factors, including high survival and rapid resprouting after burning, fire-induced mass flowering, significantly enhanced fruit and seed production in burnt and canopy-altered habitat, and greatly increased seed production in plants with larger floral displays. Additionally, support is found for characterizing *X. asphodeloides* as a primarily outcrossing species with what is highly likely to be a "leaky" self-incompatibility system. Populations typically exhibit low flowering levels in undisturbed forest which in combination with their self-incompatibility subjects them to Allee effects due to pollinator limitation in most years. Disturbance by fire results in release from these limiting factors by inducing mass flowering, altering the forest habitat and increasing pollinator activity, thus facilitating outcrossing and seed set. Finally, fire frequency, elevation, slope and forest type are indicated as the main explanantory variables for predicting suitable habitat in the classification tree/GIS model. This model correctly classifies 74% of known turkeybeard presence areas and 90% of known absence areas, and results in the discovery of eight new occupied habitat patches during ground-truthing exercises. Results of this research project are valuable not only for the conservation and management of *X. asphodeloides*, but also make a major contribution to the understanding of disturbance regimes in Appalachian forests and have important implications for improving ecologically based management efforts of these lands.

DISTURBANCE BY FIRE AND ITS ROLE IN THE POPULATION BIOLOGY AND
DISTRIBUTION OF A RARE TEMPERATE FOREST HERB


by


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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2006




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## Dedication

This work is dedicated to my parents, Norman W. and Mary L. 'Babe' Bourg, for their unwavering support, love and encouragement over the years, and to the memory of my maternal grandparents, Dominic and Mary V. Battistone, who first instilled in me an appreciation of plants and a love for nature.  They each have my eternal gratitude.

**Acknowledgements**

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**Chapter 1**


**Disturbance by Fire in the Appalachians and Its Effects on Demography and Reproduction in Turkeybeard (*Xerophyllum asphodeloides*) (L.) Nutt., a Rare Forest Herb**

**Disturbance by Fire in the Appalachians and Its Effects on Demography and
Reproduction in Turkeybeard (*Xerophyllum asphodeloides*) (L.) Nutt.,
a Rare Forest Herb**

**Abstract:**


This study comprises a comprehensive investigation of the role and effects of
disturbance by fire on the population biology of turkeybeard (*Xerophyllum asphodeloides*
(L.) Nutt., Melanthiaceae) a rare forest herb of the Appalachian Mountains.  Analyses of
long term monitoring data from a primary study population demonstrated that
turkeybeard is a long-lived, infrequently flowering perennial with high survival and rapid
resprouting ability following fire.  Effects of forest disturbance on fruit and seed
production in this population were evaluated via a controlled, fire and canopy alteration
'pulse' experiment.  Population-level flowering and inflorescence production rates
increased 60-280% in the $2^{nd}$ and $3^{rd}$ growing seasons following experimental treatment.
Fruit and seed production per inflorescence was significantly higher in experimentally
treated plants than in control individuals.  Relative isolation from other flowering plants
had no significant effect on fruit and seed production.  Additionally, plants with larger
floral displays, as measured by the number of flowering stalks produced per plant, had
much greater total seed production than single-stalked plants.  However, fruit and seed
yield/inflorescence were significantly different only in those plants that produced five or
more flower stalks, which yielded fewer fruits and seeds/inflorescence than individuals
with smaller floral displays.  Surveys of other populations and results from pollination
biology experiments showed that *X. asphodeloides* populations typically exhibited low

flowering levels in undisturbed forest and that outcrossing was needed for good seed set. The combination of these factors subjected populations to Allee effects due to pollinator limitation in most years. Disturbance by fire resulted in release from these limiting factors by altering the forest habitat to attract insect pollinators and inducing mass flowering. This research demonstrates that *X. asphodeloides* is one of the few definitively fire-adapted forest understory herbs in the eastern United States. These findings are valuable not only for their conservation and management implications, but also as a major contribution to the understanding of disturbance regimes in Appalachian forests and have important implications for improving ecologically based management of these lands.

**Introduction:**

> "Fire has been and will continue to be part of the environment of the deciduous forest region and research on its possible beneficial effects for forest and wildlife management is *urgently* needed. The deleterious effects of fire in the Southeast have been too long overemphasized and have hindered much fire research, particularly in the deciduous forest region. *There is less fire research in this area than in any other part of the country.*"
> - E.V. Komarek (1974), italics mine

A. *Overview of Fire in Appalachian Forests*

From the above quote by one of the deans of fire ecology it is clear that research on the role and effects of fire in southern Appalachian forest ecosystems has been very limited. Much of this work has been historical in nature, employing paleoecological and

dendrochronological techniques to investigate pre-European settlement fire regimes. Lorimer (2001) stated that such historical data was consistent with an assertion of frequent fire in more remote upland Appalachian oak-pine forests. Indeed, many of these studies documented recurrent prehistoric fire and remarkably similar presettlement mean fire intervals of 8 – 30 years in oak and oak-pine forests from New Jersey through the mountainous portions of Pennsylvania, Maryland, Virginia, North Carolina, and Tennessee (Lutz 1930, Buell et al. 1954, Watts 1979, Harmon 1982, Sutherland et al. 1993, Delcourt and Delcourt 1997, 1998; Frost 1998, Williams 1998, Abrams 1992, 2000, 2002, 2003; Harrod et al. 2000, Shumway et al. 2001). Most of the remaining research in the intervening years since Komarek's statement have focused largely on fire effects on overstory tree composition and structure, and to a lesser extent on species diversity and cover changes in woody shrubs and understory herbs (Barden and Woods 1976, Barden 1977, Harmon 1984, Harrod et al. 1998, 2000; Elliot et al. 1999, Waldrop and Brose 1999, Abrams 2003, Hutchinson et al. 2005a, b).

There has been much recent controversy regarding the role and influence of large-scale disturbances in eastern temperate forests, in terms of the structure and composition of both the overstory trees and the understory flora (Bormann and Likens 1979, Harmon 1982, Lorimer 1989, DeVivo 1990, Abrams 1992, Duffy and Meier 1992, Elliot and Loftis 1993 and accompanying replies, Delcourt and Delcourt 1997, Frelich 2002). Lorimer (1989) stated that research in northern hardwood-hemlock forests has documented significant impacts of catastrophic natural disturbances, often consisting of storm-related blowdowns followed by heavy fuel load-fed fires, and that episodes of

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partial stand destruction could create large gaps by removing up to 50% of the forest canopy. Skeen (1993) suggested that similar hurricane-induced forest damage followed by fire might have been responsible for the origin and maintenance of many presettlement southern pine stands. Recurring fire has been documented as a common factor associated with the domination by oak (*Quercus*) and pine (*Pinus*) species of most post-Pleistocene forests of eastern North America (Abrams 1992). Duffy and Meier (1992) concluded that spring herb species richness and cover in secondary Appalachian cove forests was significantly lower than in primary cove stands, but were severely criticized by Johnson et al. (1993) and others for not examining the disturbance history of the primary forests and for methodological errors. A number of recent studies have examined the impact of logging on these forests (Duffy and Meier 1992, Johnson et al. 1993, Gilliam et al. 1995, Meier et al. 1995) while the role of fire has been neglected.

There is increasing evidence that fire was a common and significant disturbance agent in eastern forests. Lightning strikes probably made small area fires a relatively frequent occurrence in the Appalachians (Barden 1974, Barden and Woods 1976, Komarek 1974). Native Americans also used forest fires extensively in their culture (Harmon 1982, Williams 1989, De Vivo 1990, Denevan 1992, Abrams 1992, Shands 1992, Delcourt and Delcourt 1997). A study of fossil charcoal and pollen accumulation at Horse Cove bog in the Blue Ridge mountains of North Carolina, an area historically dominated by oak-chesnut-pine forest and known to have been inhabited by Native Americans since at least 8,000 BC, showed that fire was a common disturbance agent throughout this time, with most fires being watershed-scale in size (Delcourt and

Delcourt 1997). Pyne (1982) documented the accounts of numerous early settlers that portrayed the early colonial American landscape as something drastically different from the perception of the forest primeval; rather, the forest was often difficult to traverse and settle due to the prevalence of thick regrowth in areas burned over by Native Americans and natural fires.

The diverse forests of central and southern Appalachia harbor some communities where fire is thought to be an important factor for maintenance and regeneration. Two such communities in this region are the xeric pine-oak and the table mountain pine (*Pinus pungens*) forest types, the latter of which is considered to be in range-wide decline due to fire suppression over the last century (Zobel 1969, Van Lear and Waldrop 1989, Williams and Johnson 1990, Sutherland et al. 1993, Williams 1998, Waldrop and Brose 1999). Existing fire ecology research in these communities has focused on effects on overstory trees and their regeneration, but little research has been done on their understory plant communities. Fire, however, may have a major influence on the population ecology of understory species in these fire-influenced communities. Fire as a disturbance agent alters habitats in both direct and indirect ways. Direct effects include the intense heat of combustion, the consumption of vegetation, and the deposition of ash. Indirect effects include the creation of light gaps and canopy opening, that in turn increases exposure of the understory to sunlight. Many forest understory plant species occur as groups of individuals patchily distributed within an overshadowing matrix of canopy trees (Collins et al. 1985). A number of factors including fire could play a role in

the existence of such habitat patches, particularly in communities where this disturbance agent occurred with frequency (White and Pickett 1985, Roberts and Gilliam 2003).

Studies of the fire ecology of herbaceous plants in a number of habitats have documented varied effects, both positive and negative in nature.  Effects on grass species are often very dependent upon a combination of the shade tolerance of tiller production, fire interval and fire season (Daubenmire 1968, Silva et al. 1991, Bond and van Wilgen 1996).  The massive resprouting, growth, flowering , and seeding response of fireweed (*Chamerion (=Epilobium) angustifolium*) in recently burned-over forest has long been known (Skutch 1929, Stickney 1980, 1990; Foster 1985, Morris and Wood 1989).  Fire enhanced adult growth, survival, and recruitment but not reproduction in two prairie species of *Silene* (Menges and Dolan 1998, Lesica 1999).  Fire decreased survival, however, in prairie populations of scarlet gilia (*Ipomopsis aggregata*) (Paige 1992).  In a series of detailed demographic and habitat studies of Florida scrub herbs, Menges and colleagues demonstrated that fire interval was a crucial factor in maintaining population viability and regulating metapopulation dynamics in these species (Menges and Hawkes 1998, Quintana-Ascencio et al. 1998, Satterthwaite et al. 2002, Boyle et al. 2003, Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004, Menges et al. 2006).  Additionally, Menges and Root (2004) showed that fire stimulated growth and mass flowering in a fire-adapted Florida goldenrod.  Lastly, fire had or was postulated to have contrasting effects on pollinator visitation and fruit set in a number of scrubland herb species (Ne'eman et al. 2000, Evans et al. 2003).

In terms of herbaceous species, those possessing a geophytic growth form have often been characterized as fire-adapted. This is especially true of a number of monocot families, including various members of the Liliaceae and closely related families, as well as the Iridaceae, Orchidaceae, Amaryllidaceae and the Xanthorrhoeaceae (Bond and van Wilgen (1996). Skinner and Sorrie (2002) recently described the Sandhills lily (*Lilium pyrophilum*) as a new fire-dependent species restricted to ecotonal habitats in the longleaf pine (*Pinus palustris*) sandhills ecosystem of southeastern Virginia, North and South Carolina. Fire-stimulated flowering has been recorded in the golden brodiaea lily (*Triteleia (= Brodiaea) ixioides*) of California chaparral (Stone 1951) and in the South African fynbos iris *Watsonia pyramidata* (Le Maitre 1984). The fire-lilies (*Cyrtanthus* spp., Amaryllidaceae) of South Africa flower only in the first few weeks after a fire (Keeley 1993, Bond and van Wilgen 1996). Norton and de Lange (2003) found that population size and flowering of the endangered orchid *Corybas carsei* was enhanced by fire in New Zealand peat bogs. Perhaps the plant family with the most extensive fire ecology literature base is the unusual grasstree family, Xanthorrhoeaceae (Lamont et al. 2004). Fire effects have been studied mainly in a number of Australian species in this family. Most studies have shown mass flowering and increased seed production following fire with little negative effect on grasstree plants (Gill and Ingwersen 1976, Lamont and Downes 1979, Taylor et al. 1998, Lamont et al. 2000, 2004), although Curtis (1998) did record increased long-term mortality of large individuals of one species after burning.

B.  *Turkeybeard as a Model Species*

One herbaceous understory geophyte that is often associated with southern Appalachian mixed pine-oak forest communities is turkeybeard (*Xerophyllum asphodeloides*, **Figures 1-3**), a perennial herb that occurs in disjunct mountain populations from Virginia to Alabama.  The unusual characteristics of *Xerophyllum* led Takhtajan (1997) to place the genus into its own family, the Xerophyllaceae; but the most recent systematic treatments have included it in the family Melanthiaceae within the Liliales based on combined morphological and molecular characters (Rudall et al. 2000, Zomlefer et al. 2001).  It is endangered or rare in portions of its range and is in the US Center for Plant Conservation's National Collection of Endangered Plants (CPC 2004; see distribution map in Chapter 3 or in Bourg et al. 2005), although it is not uncommon in Virginia and in the Pine Barrens of New Jersey (Harvill et al. 1977, West Virginia Natural Heritage Program 1994, 1995a, b).

The only congener of *X. asphodeloides* is beargrass (*X. tenax*), which grows more commonly in the northern Rocky Mountains, the Pacific Northwest, and northern California (Hitchcock and Cronquist 1973, Utech 1978).  Published information on the ecology of *X. tenax* in the western U.S. suggests that it possesses a number of disturbance-related characteristics.  *X. tenax* is said to be moderately shade-tolerant, seldom flowering beneath a forest canopy yet growing vigorously and blooming profusely in forest openings (Maule 1959, Mueggler 1965, Daubenmire and Daubenmire 1968, Halverson 1986).  Anecdotal claims of seven-year flowering cycles originated in

the late 19th century (Eastwood 1898, Jepson 1901) and have persisted as a confounding issue in the folklore of some localities to the present day, however (pers. obs.).  In his study of the pygmy conifer forests of Mendocino County, California, Westman (1975) classified beargrass as a heliophilic plant that did well on relatively unproductive, open sites.  Additionally, Habeck (1968) and Lotan (1986) showed that beargrass cover declined as succession proceeded in old-growth western redcedar (*Thuja plicata*) - western hemlock (*Tsuga heterophylla*) forests of Glacier National Park and in Rocky Mountain forest stands, respectively.  Studies of fire effects on *X. tenax* have documented positive responses only in survival and vegetative regrowth with the exception of intensely burned sites, and little to no evidence has yet been provided on effects on reproduction (Franklin and Dyrness 1973, Davis et al. 1980, Lyon 1984, Arno et al. 1985, Stickney 1985a, b, 1986; Hunter 1988).

**Figure 1.** Mass-flowering individuals of *X. asphodeloides*, showing large basal clumps of grass-like leaves (50mm black lens cap nested at base of plant in foreground for scale comparison), Rip Rap population, Shenandoah National Park, VA, May 2002.
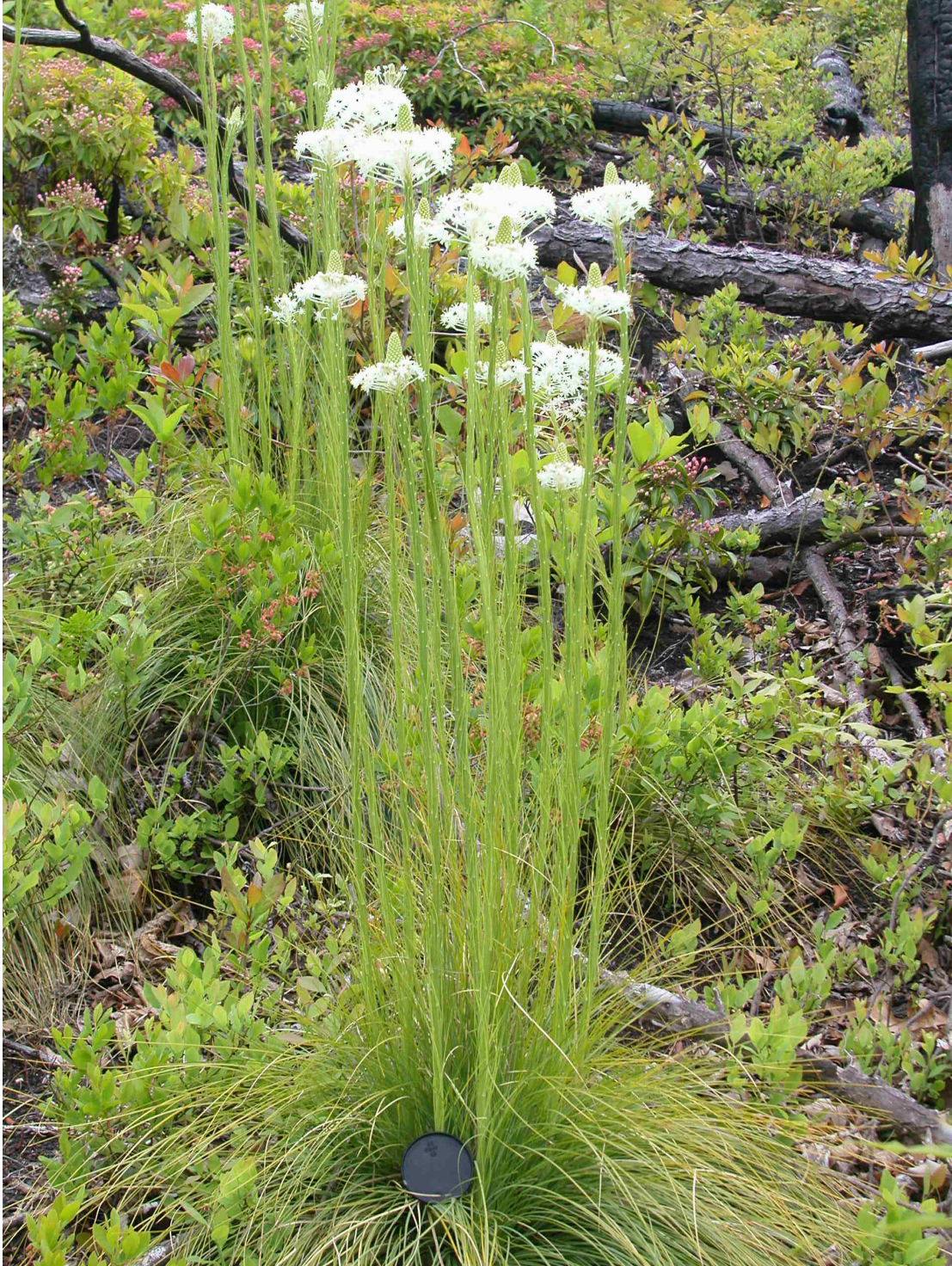
**Figure 2.** Zoomed-in view of habit of *X. asphodeloides* (50mm black lens cap nested at base of plant for scale comparison), Rip Rap population, Shenandoah National Park, VA, May 2002.

**Figure 3.** Close-up of *X. asphodeloides* inflorescences and flowers, Rip Rap population, Shenandoah National Park, VA, May 2002.

Both *X. asphodeloides* and *X. tenax* have similar morphologies that likely reflect similar life histories, although heretofore there has been little in-depth study of the ecology of either species upon which to draw comparisons. *X. tenax* is generally more robust in morphology (Utech 1978). The long and narrow, grass-like basal leaves characteristic of both species emerge from the dorsal surface of a stout subterranean tunicate bulb – rhizome structure in ramet-like whorls (Ambrose 1975); these multiply and sprout from additional meristems as an individual ages. The leaves are evergreen, persist aboveground for multiple years, and make the plants conspicuous in any season. Both species occasionally produce large flowering stalks that can reach up to 1.5 meters (*X. asphodeloides*) or 2m (*X. tenax*) tall topped by a striking 'pom-pom' of hundreds of small white flowers in a dense terminal raceme. These stalks are susceptible to at least two species of rust fungus, *Puccinia atropunctata* (Savile 1979, Zomlefer 1997) and *Uromyces veratri* (Zomlefer 1997), both of which cause a visible blackening of the stalk and premature wilting of the inflorescence. Each *X. asphodeloides* flower is capable of producing a fruit that typically contains a maximum of six seeds borne in a single deeply tri-lobed loculicidal capsule, whereas the fruits of *X. tenax* can produce twice as many seeds/capsule (Utech 1978, Zomlefer 1997).

Currently, the only published account on the ecology of *X. asphodeloides* is Bourg et al. (2005), which presented a predictive habitat model for the occurrence of turkeybeard in northwestern Virginia. This study showed that historical fire frequency was one of four main variables explaining the distribution of turkeybeard habitat at the landscape scale, with populations inhabiting areas of higher historical fire frequency.

Among the many as yet unstudied aspects of turkeybeard's ecology, however, are the population-level effects of fire. The scant anecdotal natural history accounts suggest that *X. asphodeloides* is fire-dependent, fire-resistant, or fire-tolerant (Morse 1988, Van Lear and Waldrop 1989, West Virginia Natural Heritage Program 1994, 1995a, b), but there has been no previous demonstration or experimentally validated linkage of fire to the species' population ecology. This is important for conservation management of mountain populations of turkeybeard because most occur on National Forest and National Park lands, where fire suppression has been the management policy for nearly a century.

This paper reports the results of a long-term study involving empirical population monitoring and a controlled 'pulse' experiment (Bender et al. 1984) to examine the relative effects of fire and forest canopy alteration on the ecology of *X. asphodeloides*. The experiment was initiated as part of the Orchid Hill Ecosystem Management Project (OHEMP) in conjunction with the U.S. Forest Service as the agency activated forest management plans to reduce deadwood accumulation in the aftermath of the gypsy moth (*Lymantria dispar*) invasion into Virginia in the late 1980's and early 1990's (Sharov et al. 1996). Additional supporting data on fire effects and historical fire occurrences were obtained from a number of other turkeybeard populations occurring in the northern Ridge and Valley and Blue Ridge physiographic provinces of Virginia (Harvill et al. 1977), namely within the boundaries of the George Washington National Forest (GWNF) and Shenandoah National Park (SNP). The specific objective of this study was to test the following three null hypotheses regarding the response of *X. asphodeloides* to experimental manipulation:

1. *The Fire/Canopy Alteration Effect Hypothesis* - There is no difference in the reproductive performance of plants in the three treatment categories of control (shaded/no fire) vs. canopy intact (shaded/fire) vs. canopy-altered (open/fire) quadrats.

2. *The Floral Density Effect Hypothesis* - There is no difference in the reproductive performance of isolated flowering plants vs. flowering plants occurring in clumps with other flowering individuals.

3. *The Floral Display Effect Hypothesis* – Plants that produce more inflorescences do not experience lower reproductive performance per flower stalk.

**Study Sites and Methods:**

*Long-term study population:*

Fourteen years of demographic data on a turkeybeard population located at the OHEMP long-term study site on the Dry River Ranger District of the GWNF, Virginia (Gill 1989, 1996) served as a foundation for the experiment. The site, known as Orchid Hill, lay on an east-west running spur ridge at an elevation of 763m (**Figure 4**). The mixed conifer-hardwood forest here was dominated by table mountain pine, chestnut oak

**Control Grid:**

| | | AAo | AA | BB | CC | DD | EE | FF | GG |
|---|---|---|---|---|---|---|---|---|---|
| C | Row 9 | | | | | | | 3 | 1 |
| C | " " 8 | | | | | | | 1 | 5 |
| C | " " 7 | | | | | | | 4 | 7 |
| C | " " 6 | | | | 1 | | 1 | 2 | 5 |
| C | " " 5 | | | 2 | 3 | 6 | | 8 | 1 |
| C | " " 4 | | | | | 1 | 9 | 10 | |
| C | " " 3 | | | | 2 | 6 | 27 | 3 | |
| C | " " 2 | | | 2 | | 6 | 2 | | |
| C | " " 1 | 1 | | | | | 1 | | |

**Dirt Road (FR 72)**

N

**Experimental Grid:**

| | | Ao | A | B | C | D | E | F | G | H | I | J | K |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Strip 1 - SF | Row -3 | | 2 | | | | 2 | | | | | | |
| Strip 1 - SF | " " -2 | | 3 | | | | | 5 | | 1 | | | |
| Strip 1 - SF | " " -1 | | | | | 4 | | 1 | | 1 | | | |
| Strip 1 - SF | " " 0 | | | | | 2 | 6 | 1 | | 5 | | 3 | |
| Strip 1 - SF | " " 1 | | | | | 1 | 1 | 1 | 6 | 2 | | | |
| Strip 1 - SF | " " 2 | | | | | 1 | 2 | 3 | 4 | 4 | 1 | | |
| Strip 1 - SF | " " 3 | | 4 | 1 | | | 1 | 2 | 3 | | | | |
| Strip 1 - SF | " " 4 | 1 | 2 | 2 | 2 | 1 | 4 | | 8 | 1 | 3 | 3 | |
| Strip 1 - SF | " " 5 | | | 1 | 1 | | 5 | 2 | 4 | 5 | | 1 | |
| Strip 1 - SF | " " 6 | | | | 1 | 1 | 2 | 2 | 3 | 1 | | | |
| Strip 2 - OF | " " 7 | | 2 | 2 | 1 | 3 | 1 | 3 | 2 | | | | |
| Strip 2 - OF | " " 8 | | 5 | 2 | 2 | | | | 1 | 1 | 3 | 1 | |
| Strip 2 - OF | " " 9 | | | | | | | 2 | | | | | |
| Strip 2 - OF | " " 10 | | 6 | | | 7 | 1 | 5 | 6 | 2 | 1 | 1 | |
| Strip 2 - OF | " " 11 | | 1 | 1 | 21 | 10 | 2 | 4 | 2 | 1 | 2 | | |
| Strip 2 - OF | " " 12 | | | | 13 | 3 | | 14 | | 2 | 1 | | |
| Strip 3 - SF | " " 13 | | | | | 1 | 6 | 9 | 1 | 4 | | | |
| Strip 3 - SF | " " 14 | | | | 1 | 2 | 2 | 3 | 9 | | 3 | 1 | |
| Strip 3 - SF | " " 15 | | | 2 | 1 | | 1 | 1 | 4 | | | 1 | |
| Strip 3 - SF | " " 16 | | | | | 1 | 4 | 1 | 2 | | 1 | 4 | |
| Strip 3 - SF | " " 17 | | | | | 2 | 2 | 3 | | | | 6 | |
| Strip 3 - SF | " " 18 | | | | 2 | 5 | 1 | | | 3 | | 5 | |
| Strip 4 - OF | " " 19 | | | | | | | 1 | 2 | 2 | 2 | 3 | 1 |
| Strip 4 - OF | " " 20 | | | 2 | | | 4 | 3 | | 3 | 5 | 3 | 7 |
| Strip 4 - OF | " " 21 | | | | | | | 1 | 11 | 5 | 14 | 7 | 3 |
| Strip 4 - OF | " " 22 | | | | | 1 | 1 | | 5 | 7 | 22 | 5 | 1 |
| Strip 4 - OF | " " 23 | | | | 2 | 5 | | | 2 | 7 | 4 | 6 | 1 |
| Strip 4 - OF | " " 24 | | | | | | | | 11 | 5 | 4 | 2 | 1 |
| Strip 4 - OF | " " 25 | | | | | | 1 | 1 | 6 | 2 | 3 | 6 | |

**Figure 4.** General location (inset) and simplified map of the long-term study grid at Orchid Hill, GWNF, Rockingham Co., VA. Each cell represents a 4x4m quadrat, with the numbers of marked turkeybeard plants in each cell shown. Beginning in 1996, C = Control, SF = shaded/fire, and OF = open/fire treatment. The crest of the spur ridge runs down columns C and D.

(*Quercus montana(= prinus)*), and pitch pine (*P. rigida*) with an understory shrub layer

composed mainly of bear oak (*Q. ilicifolia*), early low-bush blueberry (*Vaccinium*

*vacillans*), black huckleberry (*Gaylussacia baccata*), mountain laurel (*Kalmia latifolia*),

and mountain fetterbush (*Pieris floribunda*).  The 0.4-hectare study area was permanently

gridded with iron rebar into 192 4x4-m quadrats.  Turkeybeard plants were marked at the

site using individually numbered galvanized steel or aluminum tags inserted into the

ground adjacent to the base of each plant with a 20d nail.  Location, condition, size and

flowering data were recorded.  From 1990 to present, all flowering plants were marked,

so that population reproductive data were complete for this period.  Beginning in 1996,

systematic surveys of the experimental grid resulted in flowering and non-flowering

plants being marked.  Survival data therefore extended back to 1990 only for a portion of

the marked individuals.  Beginning in 1996, 48 more quadrats were demarcated with

wooden stakes in unmanipulated forest adjacent to the experimental grid and plants here

were marked and measured in identical fashion.


*Habitat manipulation experiment:*


Preparation for the habitat alteration experiment at the Orchid Hill study site

began in autumn 1994 when canopy tree girdling treatments were placed in separate 24m

wide x 32m long strips (Strips 2 and 4) at the site.  Cutting through the bark and cambium

near the trunk's base with a hand axe or chainsaw girdled large trees in these strips.

Selective felling of smaller trees and large shrubs was also employed to remove the

canopy layer.  These techniques were employed to create a treatment that mimicked the

canopy removal aspect of a stand-replacing fire while at the same time protecting against

the high potential for escaping wildfire at the mountainous, heavily forested locality of

Orchid Hill. Two other 24m x 32m strips that had their canopies left intact (Strips 1 and

3) alternated with the canopy removal strips. After allowing for above-ground canopy

tree mortality to occur in the girdled strips during the 1995 growing season, a low

intensity prescribed fire (flame heights 0.3 - 1m, rate-of-spread 0.3 – 2.5 m/s; Slater

1996), ignited by drip torch and delayed aerial ignition devices (DAIDs, i.e., potassium

permanganate and ethylene glycol-filled ping-pong balls), was conducted over the entire

study site under the coordination of the U.S. Forest Service (USFS) on April 22, 1996.

Thus, four categories of quadrats subject to controls and/or treatments were available for

evaluation:


1) Pre-burn - data from 1991 through 1995 (no fire during this period with

temporary canopy opening due to gypsy moth defoliation from 1990 through

1991; canopy recovered and intact from 1992 through 1994; and canopy opening

transition from 1994 through 1995),


2) Control (C) - data from 1996 through 2005 (no fire with canopy intact),


3) Shaded Fire (SF) treatment – fire with canopy intact from 1996 through 2005,

and


4) Open Fire (OF) treatment - fire with canopy removed from 1996 through 2005.

Samples of mature turkeybeard inflorescences were collected from the study site in post-experiment years and fruit and seed production on each was evaluated in the laboratory to address the stated reproductive performance hypotheses. Only plants that produced single flower stalks were used to test the Fire/Canopy Alteration Effect hypothesis and the Floral Density Effect hypothesis to avoid any confounding effect of multiple flower stalk production on these analyses. To define categories for the Floral Density hypothesis, a plant was designated 'isolated' if there was no more than one other flowering individual within 4m (one quadrat ) of it. This definition could not be made more exclusive due to the sheer numbers of flowering individuals in the two post-experiment response years. Five flowering stalk classes comprising 1, 2, 3, 4 and $\geq$5-stalked plants were designated for testing the floral display effect hypothesis. The fruit and seed count data were analyzed using SAS Version 9.0 statistical software (SAS Institute Inc. 2002) as unbalanced, incomplete block design, mixed-model analyses of covariance (ANCOVAs), with the total number of flowers per inflorescence specified as the covariate. The main blocking factors were year, infection of flower stalks with a rust fungus, plant vegetative size, flowering stalk height, and slope exposure (north, south or east-facing). Count data were square root-transformed where necessary to meet the ANCOVA assumptions of homogeneity of variances and normality. In those instances where a significant main effect by covariate interaction was found, main effect categories with parallel slopes were grouped together and paired comparisons with the remaining main effect categories were estimated over four values of the covariate (i.e., first quartile = 25%, median = 50%, mean, and third quartile = 75%), as recommended by Littell et al. (1996). Similar inflorescence samples were collected from a population located 2.2km

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away at 683m elevation in 1998 and 1999, as well as a second population 3.5km away at 610m in 1999, to have baseline data from undisturbed populations with which to compare reproductive performance in the Orchid Hill control plants using the same analysis methods.

To compare general flowering levels in the Orchid Hill population with other turkeybeard populations in the region, informal walking transect counts were conducted in several nearby populations beginning in 1997 as time permitted.  During these walks only plants that were large enough to be readily noticeable were counted in a roughly 1m swath on either side of the observer over an indeterminate distance.  In addition, during the 2000 field season formal line transect surveys were done in 22 *X. asphodeloides* populations using replicate 50- meter x 2-meter strip transects spaced at least 100 meters apart on the ground.  Three formal transects were done in each population except for two sites, where only two transects were surveyed due to time and size/shape constraints, respectively.  This resulted in areal samples of 200 - 300 $m^2$ in each population.  Plants were counted in five meter sections along each transect and the number of flowering individuals and inflorescences was also tallied.  One additional population was discovered and surveyed in this manner in 2001, and total direct counts of plants were conducted in two more populations of small areal extent in 2000.  Lastly, in May 1999 two of these populations burnt in separate escaped prescribed fires and were subsequently monitored with line transects in the 2001 and 2002 seasons.

*Fire history of turkeybeard populations:*

To investigate the possibility of past fire occurrence at the Orchid Hill study site, searches were conducted in the forest beyond the perimeter of the permanent grid to identify trees with fire-scarred (usually 'cat-faced') trunks (Arno and Sneck 1977). Cross-sections of these fire-scarred trunks were collected with a chainsaw, sanded with a hand-held electric belt sander via consecutive application of coarse, medium and fine-grained sandpapers, and then the age of the tree and year of occurrence of fire scars were recorded by counting annual tree rings. Subsequently, the fire histories of six additional turkeybeard population sites on the Dry River Ranger District of the GWNF were examined using the same methodology.

**Results:**

Long-term demography and survival:

Five hundred and sixty-eight individuals of turkeybeard were tagged in the Orchid Hill experimental grid through 2005, and 207 of these plants had monitoring records dating back to 1990. One hundred and twenty-two additional plants belonging to the same population were marked in the adjacent unmanipulated control grid from 1996 through 2005. Actual ages of these plants were unknown, so the groups were considered mixed-age cohorts. Survivorship was high throughout this period for adult-sized plants

except in 1999, and there was little difference between the survival pattern of the original

1990 pre-burn experimental grid cohort and the 1996 unburned control cohort (**Figure 5**).
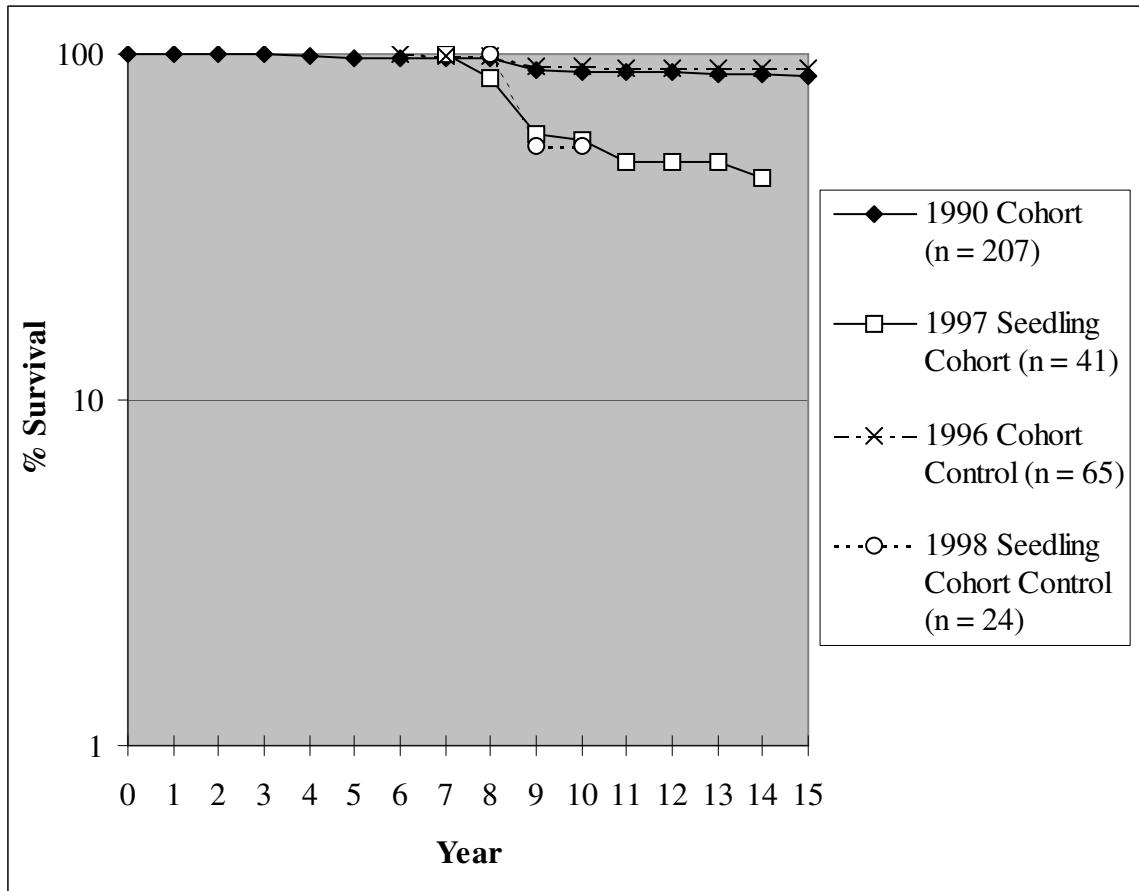


**Figure 5**. Depletion curves for adult-sized plants and seedlings of *X. asphodeloides* in the experimental and control strips respectively at the Orchid Hill long-term study site, 1990 (Year 0) – 2005 (Year 15).

The annual rate of depletion for both of these cohorts was slightly more than 1%, and the

median life expectancy was estimated to be 49 years (1990 cohort: y = -1.0685x +

102.22, $R^2 = 0.87$; 1996 cohort: y = -1.1002x + 105.09, $R^2 = 0.76$). The pattern of

seedling survivorship was considerably different than that of the more mature plants, with

substantial mortality of at least 40% in the initial 1-2 years after emergence aboveground

before stabilization toward more gradual losses in subsequent years. Mortality was

similar between the experimental grid 1997 seedling cohort and the control 1998 seedling

cohort however, and once again most deaths occurred in the 1999 season. The annual

rates of depletion for these seedling cohorts were 7 and 23%, and median life expectancy

ranged between 9.8 and 12 years (1997 cohort: $y = -7.288x + 137.8$, $R^2 = 0.77$; 1998

cohort: $y = -22.917x + 275.69$, $R^2 = 0.75$). Two of the seedlings discovered in 1997

flowered for their first time during the census period, one in 2003 and the other in 2004,

thus documenting a first age of reproduction of at least 6-7 years for *X. asphodeloides*.


The removal of small trees during installation of the canopy alteration treatment

in October 1994 caused partial canopy opening during the 1995 growing season.

Complete canopy opening, however, did not occur until the 1996 growing season because

it took a full year for the canopies of the large pines and oaks to die back. The low

intensity prescribed fire treatment in April 1996 then successfully top-killed (~ 80%

above-ground mortality) the shrub and understory layers and reduced the fuel loading of

1-hour and 10-hour fuels by 50% (Slater 1996). The thin aboveground leaves of

individual turkeybeard plants ignited readily and were burned away by the fire, but new

leaves resprouted from their subterranean bulbs within one month of the fire (**Figure 6**).

No turkeybeard mortality could be attributed to any direct effects of the fire, nor could

enhanced seed germination be unequivocally attributed to the fire and canopy removal

treatments. Although a substantial incidence of seedling establishment occurred in the

open/fire treatment strips in 1997 with 41 seedlings emerging, a somewhat lower but still

substantial seedling appearance happened in the control strip in 1998, where 24 seedlings

were recorded. These occurred in fairly discrete patches in both cases and were the only

two significant seedling emergence events observed in the post-experiment years.

**Figure 6.** *X. asphodeloides* plants with resprouting leaves approximately one month after fire, GWNF, Rockingham Co., VA.

Germination trials on random samples of 100 seeds from 32 individuals, undertaken both

in controlled growth chamber conditions following the methodology for *X. tenax*

presented by Smart and Minore (1977) in 1999 as well as in the ambient overwintering

environment of College Park, MD in 2000, produced only two seedlings, both of which

failed to survive transplantation.  Such difficult germination has been mentioned for *X.*

*asphodeloides* ( B. Cullina and C. Mattrick, New England Wildflower Society, pers.

comms.) and also noted for *X. tenax* by Vance et al. (2004).


Reproductive performance:


*1. Flowering and inflorescence production:*


Baseline flowering levels in the five years prior to experimental manipulations at

Orchid Hill were consistently low across the prospective experimental strips, reaching a

maximum of 17 flowering genets and 22 inflorescences in Strip 1 in 1994.  The

maximum number of inflorescences any plant ever produced during this pre-experimental

period was four.  In contrast, the turkeybeard population produced immense flowering

displays in the treatment strips in 1998 and 1999, the second and third post-burn years,

both in terms of the number of reproductive individuals and the inflorescences they

produced (**Figure 7**).  The maximum number of inflorescences produced by a plant was

ten, achieved by a different and lone individual in each of these major response years.

The number of flowering plants in the experimental strips was 60-270% greater in these

two years than in the next highest flowering season in the sixteen-year dataset, and

inflorescence production was 80-280% greater.  Even more striking was the observation

that the 1998 and 1999 flowering levels were five to nine times greater than typical

seasons.  These mass-flowering events were followed by a return to several years of low-level flowering similar to the pre-experimental years, with an increase to modest levels of flowering in the most recent years of 2004 and 2005.
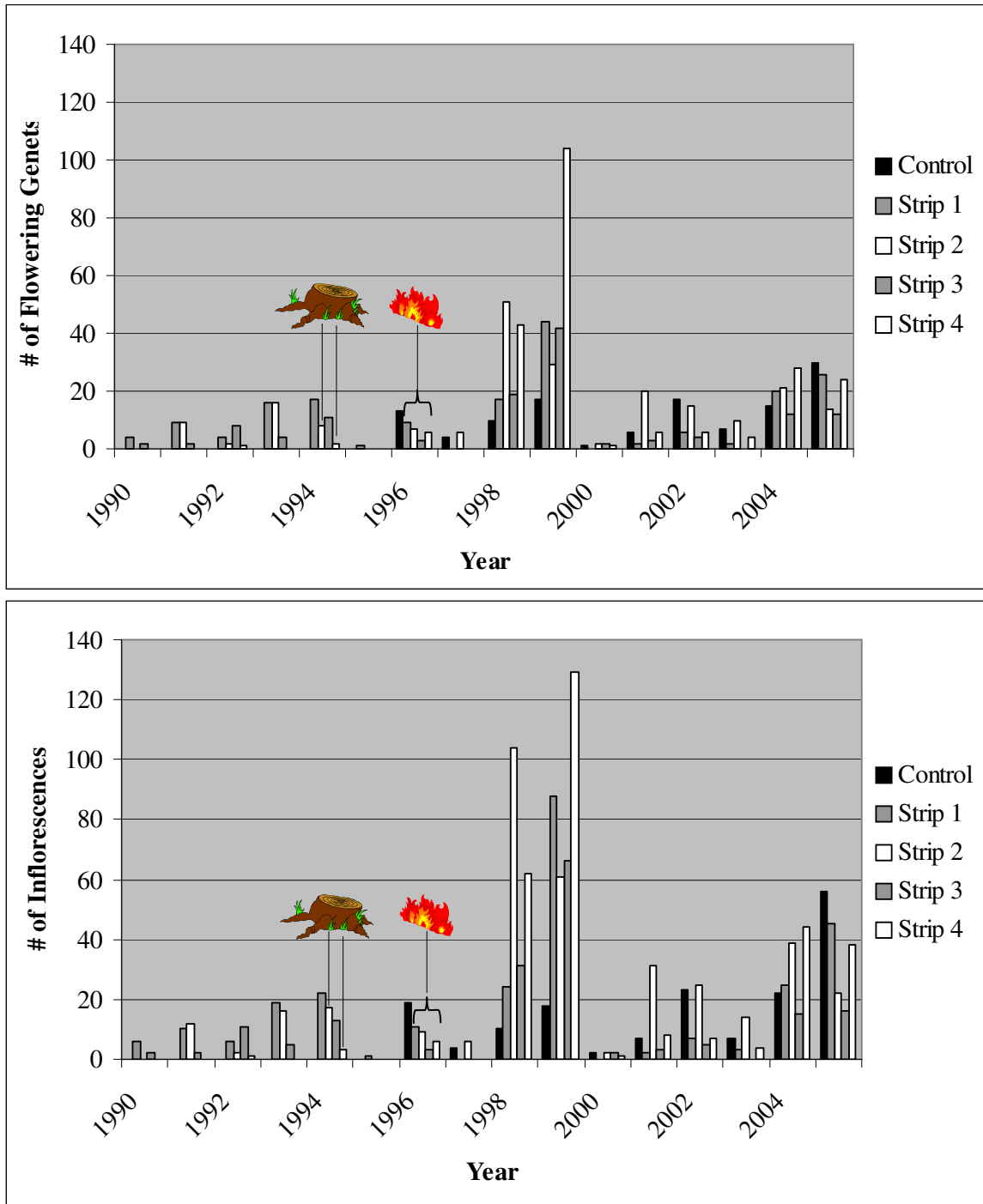
**Figure 7. Top)** Number of flowering genets, and **bottom)** inflorescence production in the *X. asphodeloides* population at the Orchid Hill study site, Dry River Ranger District, George Washington National Forest, Rockingham County, VA, 1990 – 2005. Strips 1 and 3 – shaded, canopy intact/fire; strips 2 and 4 – open, canopy removed/fire. Censuses of the control strip began in 1996. As indicated by the graphics, canopy tree girdling occurred in October 1994 in strips 2 and 4 only, and a prescribed fire was conducted in April 1996 over all four experimental strips.

Low to moderate flowering percentages also typified the subset of undisturbed populations surveyed by informal walking transects in 1997 – 1999 and 2001 (**Table 1**). The systematic line transect surveys and direct census counts of all 25 turkeybeard populations including Orchid Hill, conducted in part for a related study (Bourg et al. 2005) in 2000 and 2001, documented a wide range of population sizes but low flowering densities across the region.  Additionally, the repeated post-fire line transect surveys of the Rip Rap and Hone Quarry Ridge populations showed that both experienced large mass flowering events in the 2001 and 2002 seasons after burning in 1999, providing independent confirmation of the 2-3 year lagged mass flowering effect following fire that occurred in the Orchid Hill population.  Astonishingly, in the very large Rip Rap population in 2002, there were many turkeybeard plants that produced at least ten flowering stalks and the maximum number observed was 27 stalks on one individual. Both populations also had very low flowering in the 2003 season (pers. obs.), mirroring the low reproduction that was observed at Orchid Hill in 2000 after its prior two consecutive mass flowering years.

**Table 1.** Areal extent, plant densities, and population size estimates for 25 surveyed populations of *X. asphodeloides* on the GWNF and SNP, Virginia. † Densities from two 50 x 2 m linear transects; ‡ densities from direct counts; ˆin SNP; * = not surveyed.

| Population | Areal Extent (m²) | Total Plant Density (#/m² ± 1SE) | Flowering Plant Frequency (% with sample size or #/m² ± 1SE) | | | | | | Estimated Population Size |
|---|---|---|---|---|---|---|---|---|---|
| | | | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | |
| Rader Mtn.[†] | 1,261,479 | 0.35 ± 0.23 | * | * | * | 0.00 ± 0.00 | * | * | 441,518 ± 290,140 |
| New Market Gap | 817,208 | 0.22 ± 0.08 | * | * | * | 0.00 ± 0.00 | * | * | 179,786 ± 65,377 |
| Third Mtn. | 305,851 | 1.49 ± 0.23 | * | * | * | 0.00 ± 0.00 | * | * | 455,718 ± 70,346 |
| Mud Pond Gap | 261,524 | 0.65 ± 0.16 | 4.7 (n=85) | * | * | 0.004 ± 0.00 | * | * | 169,991 ± 41,844 |
| Feedstone Mtn. | 251,399 | 1.47 ± 0.58 | 18.6 (n=500) | 7.6 (n=500) | 34.0 (n=259) | 0.02 ± 0.01 | 1.5 (n=330) | * | 369,557 ± 145,811 |
| Rocky Run | 210,020 | 0.23 ± 0.05 | * | * | * | * | 0.00 ± 0.00 | * | 48,305 ± 10,501 |
| Big Bald Knob | 146,872 | 0.86 ± 0.04 | * | * | * | 0.037 ± 0.02 | * | * | 126,310 ± 5,875 |
| Dyers Knob | 99,716 | 0.46 ± 0.21 | * | * | * | 0.00 ± 0.00 | * | * | 45,869 ± 20,940 |
| Rip Rap[ˆ] | 67,890 | 0.54 ± 0.07 | * | * | * | 0.003 ± 0.00 | 0.28 ± 0.01 | 0.46 ± 0.03 | 36,661 ± 4,752 |
| Long Run Bottom | 55,185 | 1.51 ± 0.48 | * | * | 20.0 (n=315) | 0.00 ± 0.00 | * | * | 83,329 ± 26,489 |
| Benchmark3 | 48,130 | 0.45 ± 0.06 | * | * | * | 0.00 ± 0.00 | * | * | 21,659 ± 2,888 |
| The Knobs | 35,965 | 1.16 ± 0.45 | * | * | * | 0.00 ± 0.00 | * | * | 41,719 ± 16,184 |
| Benchmark2 | 35,052 | 0.26 ± 0.15 | * | 0.8 (n=128) | 10.4 (n=269) | 0.00 ± 0.00 | * | * | 9,114 ± 5,258 |
| Powerline | 33,162 | 0.14 ± 0.02 | * | * | * | 0.00 ± 0.00 | * | * | 4,643 ± 663 |
| Narrowback Mtn. | 25,702 | 0.37 ± 0.08 | * | * | * | 0.00 ± 0.00 | * | * | 9,510 ± 2,056 |
| Second Mtn. | 18,718 | 0.58 ± 0.13 | * | * | * | 0.00 ± 0.00 | * | * | 10,856 ± 2,433 |
| North River | 17,556 | 0.36 ± 0.16 | * | * | * | 0.003 ± 0.00 | * | * | 6,320 ± 2,809 |
| Black Run | 17,315 | 0.33 ± 0.06 | * | * | 10.4 (n=231) | 0.00 ± 0.00 | * | * | 5,714 ± 1,039 |
| Benchmark1 | 14,910 | 0.32 ± 0.05 | * | 7.7 (n=182) | * | 0.00 ± 0.00 | * | * | 4,771 ± 746 |
| Orchid Hill | 14,809 | 0.24 ± 0.07 | * | * | * | 0.00 ± 0.00 | * | * | 3,554 ± 1,037 |
| Shenandoah Mtn.2 | 7,469 | 0.49 ± 0.16 | * | * | * | 0.007 ± 0.01 | * | * | 3,660 ± 1,195 |
| Timber Ridge[†] | 6,582 | 0.38 ± 0.08 | * | * | * | 0.005 ± 0.01 | * | * | 2,501 ± 527 |
| Hone Quarry Ridge[‡] | 4,667 | 0.03 | * | * | * | 0.00 | 0.02 | 0.009 | 157 |
| Shenandoah Mtn.1 | 2,510 | 0.47 ± 0.05 | * | * | * | 0.003 ± 0.00 | * | * | 1,180 ± 126 |
| Elliot Knob[‡] | 1,638 | 0.05 | * | * | * | 0.00 | ˆ | * | 85 |

High herbivory on developing but pre-anthesis inflorescences was recorded in only the Feedstone Mountain population during the 1997, 1998, and 2001 seasons. These herbivory levels reached 97.8%, 78.9%, and 100% of all sampled inflorescences respectively in these years. In virtually every instance the entire inflorescence in bud had been eaten and the neatly sheared off nature and height of the bite mark indicated white-tailed deer (*Odocoileus virginianus*) as the effecting herbivore. Surveys of this population in 1999 and 2000 were conducted before flower stalks and inflorescences had developed enough to be browsed by deer to document herbivory in these two intervening years. Similar instances of herbivory were only rarely observed at Orchid Hill and in the other surveyed turkeybeard populations.

The pattern of flowering frequency among individuals in the Orchid Hill population over the period 1990 – 2005 showed that nearly one-third (30.7%) of the plants never flowered, and 45.8% flowered only once (**Figure 8**). Multiple flowerings by individual plants were considerably more rare, with the extreme being a single individual that flowered nine times in these sixteen years. The smallest individual that ever flowered was a plant that had a maximum leaf length of 36 cm. This observation suggested a minimum size for maturity (flowering) Therefore, the seedling/juvenile category was defined as any nonreproductive plant with a longest leaf length $\leq$ 35cm. Two-thirds of the non-flowering individuals were in this category, thus comprising approximately 17% of the long-term marked population. Notably, 36.4% of all the plants that had ever produced an inflorescence during the monitoring period were those that had reproduced for their first time in the mass-flowering years of 1998 or 1999.
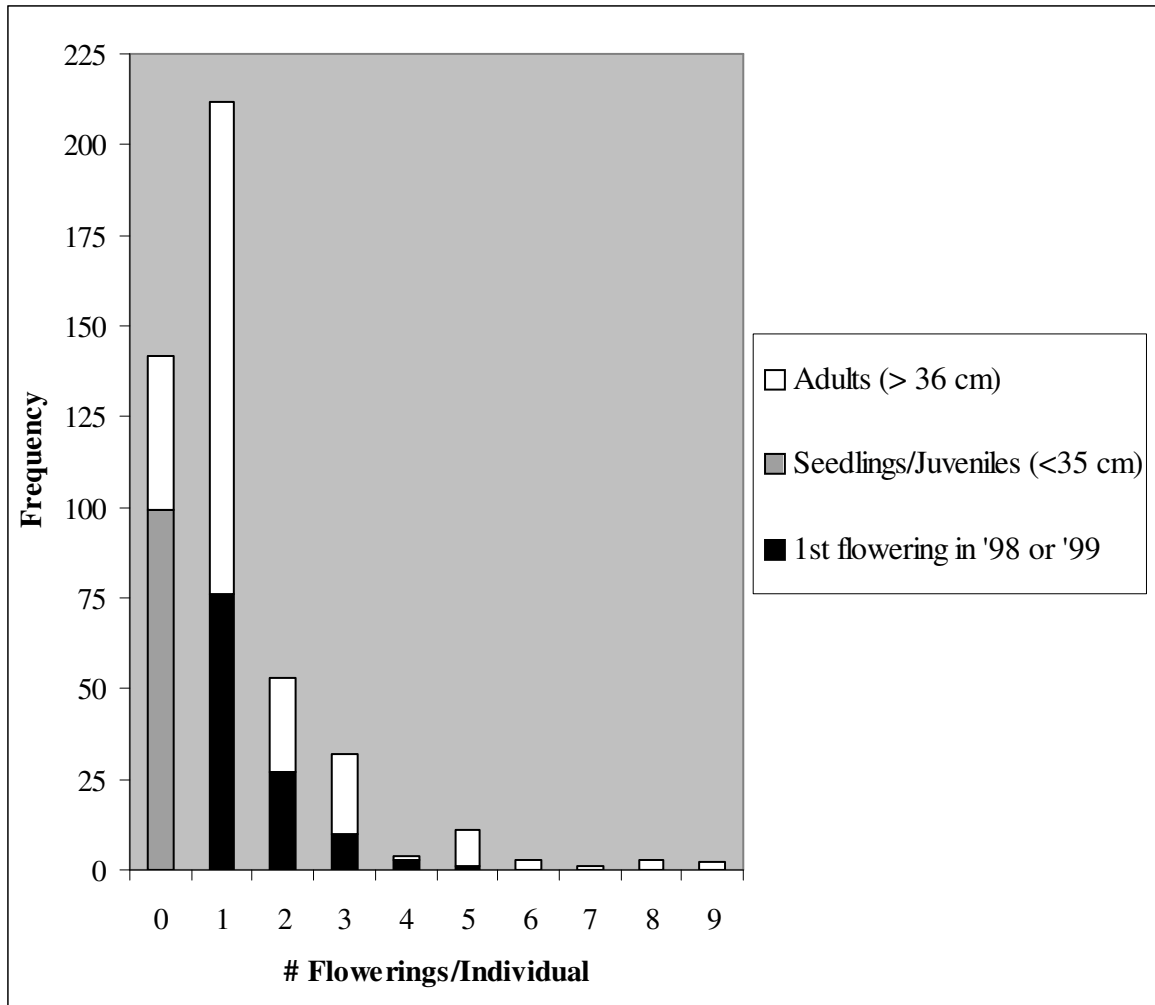
**Figure 8.** Frequency of flowering among individuals of *X. asphodeloides* in the Orchid Hill population, 1990 – 2005.

Compilation of the intervals between flowerings for individual plants at Orchid Hill from 1990 – 2005 showed no strong evidence for cyclic reproduction among plants that had flowered at least twice during this period (**Figure 9**). The one-year interval category, i.e., plants that flowered in two consecutive years at least once, contained the largest number of reproductive individuals. Forty (41.7%) of these were plants that flowered in both mass-flowering years of 1998 and 1999. The frequency decreased substantially and regularly in subsequent intervals, except for intervals 5 and 6, where moderate spikes appeared. These spikes were anomalies arising from the fact that the

mass-flowering years of 1998 and 1999 happened between five and six years after the pre-experimental high flowering years of 1993 and 1994 as well as five and six years before the relatively high flowering years of 2004 and 2005.  Yet, very few plants were repeaters in the 5-year interval category and no plants were repeaters in the 6-year interval category.  In fact, there was little indication of any particular periodicity to flowering, as those plants that repeated an interval were infrequent and were spread over each of the first five interval categories.  Two plants that remained in a vegetative state for 12 years before flowering for a second time in the 13th year displayed the most extreme interval length.
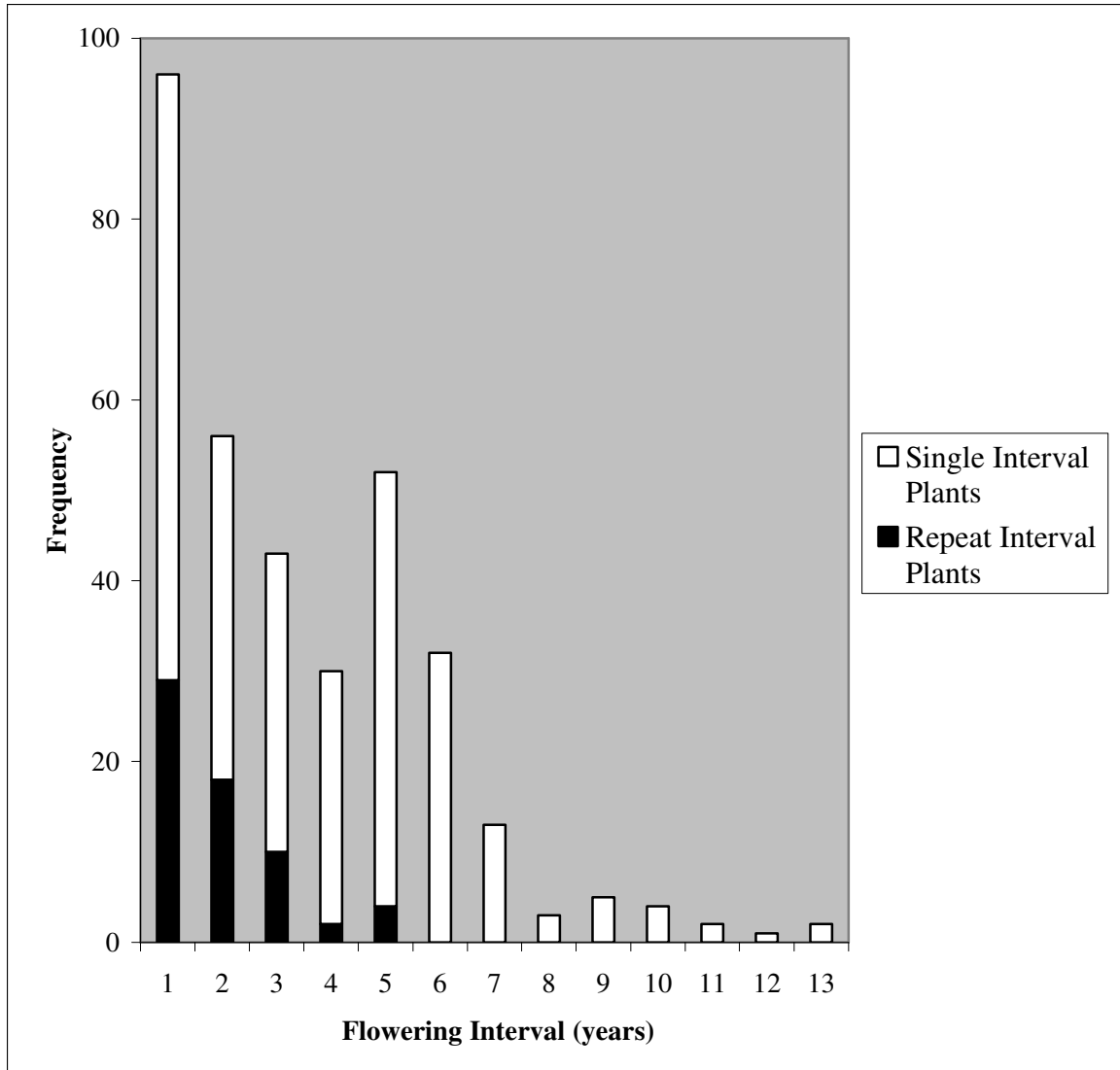
**Figure 9.** Flowering periodicity (interval in years between flowering events) among individuals of *X. asphodeloides* that flowered at least twice in the Orchid Hill population, 1990 – 2005.

## 2. Fruit and seed production - habitat manipulation experiment:

ANCOVA analyses of fruit production in 115 single inflorescence plants from 1998 and 1999 using inflorescence size (total number of flowers/inflorescence) as the covariate showed a highly significant effect of this variable in all treatment categories – i.e., the larger the inflorescence the greater the fruit production (**Table 2; Figure 10**).

The open/fire (OF) treatment performed the best, achieving from 78–86% of the maximum possible fruit production across the range of inflorescence sizes, while the shaded/fire (SF) plants performed somewhat less well at 67-73% of the maximum. The unburned, shaded control plants had the poorest fruit set, reaching from 38-52% of the potential maximum as inflorescence size increased. The covariate by treatment interaction was significant as well, largely because the slope of the shaded/fire treatment was less than the control and still less than the open/fire treatment. Both of the treatment groups had very significantly greater fruit production than the controls over the entire range of the covariate, although the overall treatment main effect was barely non-significant due to nearly identical values for shaded/fire and open/fire plants on small inflorescences. Overall, small inflorescences on plants that received fire had twice the fruit set of unfired control plants but had similar fruit production regardless of the influence of canopy opening, while the imposition of canopy opening with fire resulted in increased fruit yield for larger inflorescences.

**Table 2.  A)** Summary ANCOVA table for the effects of treatment (see also **Figure 10**) and isolation on fruit production in 115 single inflorescence plants in the experimental response years of 1998 and 1999 at the Orchid Hill study site.  Total number of flowers/inflorescence (Totfl) was used as the covariate.  **B)**  Paired treatment comparisons for the significant covariate by treatment interaction (C = control, OF = open canopy/fire treatment, SF = shaded canopy/fire treatment; $\propto$ = 0.05).

**A)**                                       Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Treatment | 2 | 103 | 2.88 | 0.0608 |
| Isolation | 1 | 95.6 | 3.50 | 0.0646 |
| Treatment*Isolation | 2 | 96.1 | 1.36 | 0.2605 |
| Totfl | 1 | 100 | 128.69 | <.0001 |
| Totfl*Treatment | 2 | 104 | 4.69 | 0.0113 |

**B)**

| Comparison | Estimate | Error | DF | t Value | Pr > |t| |
|---|---|---|---|---|---|
| OF-C at 25%=167 | 67.1768 | 15.1672 | 98.6 | 4.43 | <.0001 |
| OF-C at 50%=206 | 75.8265 | 12.7162 | 96.4 | 5.96 | <.0001 |
| OF-C at mean=221.4 | 79.2376 | 12.7258 | 96.9 | 6.23 | <.0001 |
| OF-C at 75%=270 | 90.0208 | 16.2444 | 101 | 5.54 | <.0001 |
| SF-C at 25%=167 | 59.6861 | 14.6581 | 99.3 | 4.07 | <.0001 |
| SF-C at 50%=206 | 52.5564 | 12.1908 | 96.8 | 4.31 | <.0001 |
| SF-C at mean=221.4 | 49.7448 | 12.4072 | 97.1 | 4.01 | 0.0001 |
| SF-C at 75%=270 | 40.8565 | 16.9634 | 101 | 2.41 | 0.0178 |
| OF-SF at 25%=167 | 7.4907 | 12.1195 | 99 | 0.62 | 0.5379 |
| OF-SF at 50%=206 | 23.2700 | 9.6516 | 94.6 | 2.41 | 0.0178 |
| OF-SF at mean=221.4 | 29.4928 | 9.3211 | 93.1 | 3.16 | 0.0021 |
| OF-SF at 75%=270 | 49.1644 | 11.0709 | 95 | 4.44 | <.0001 |
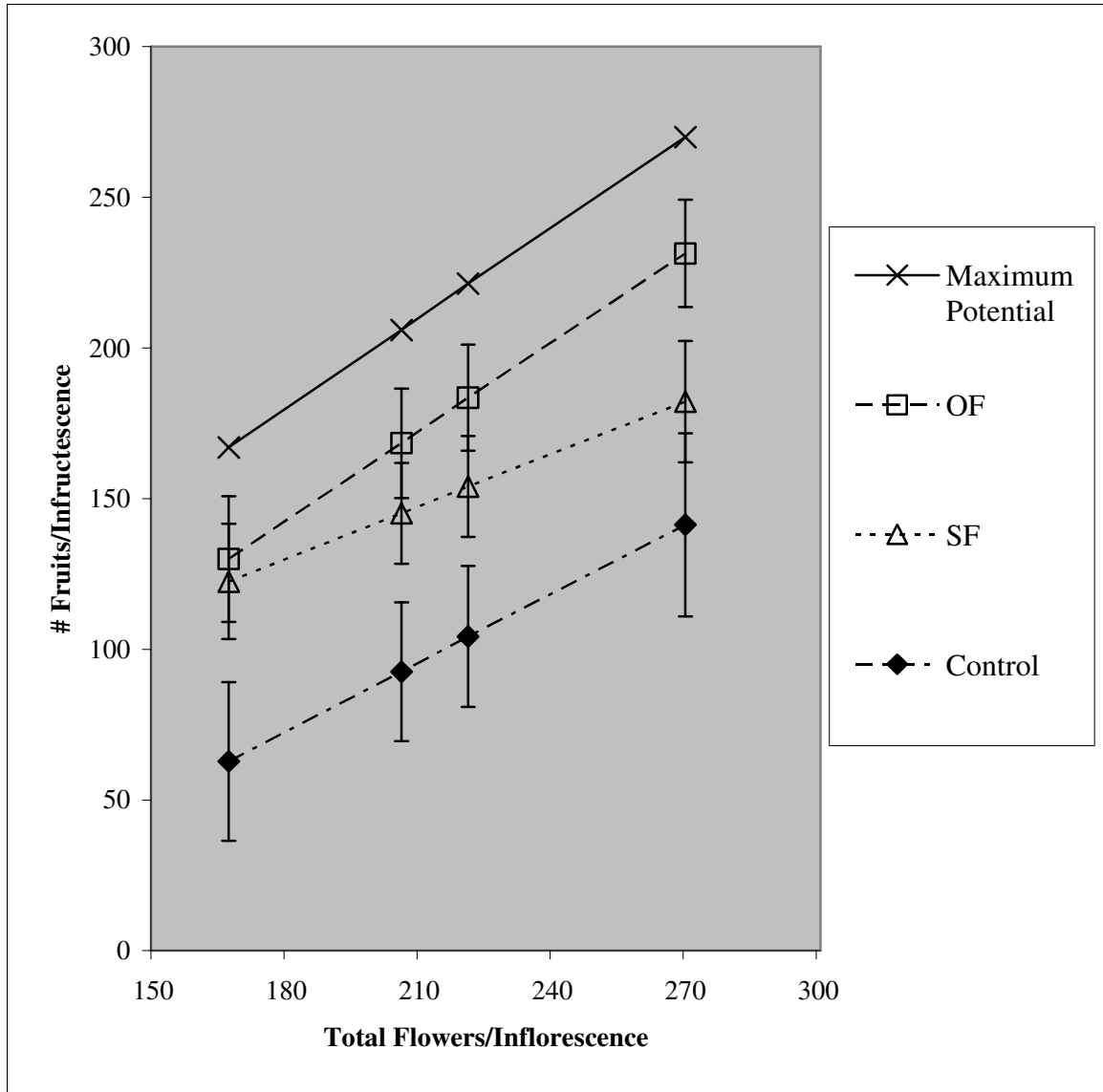
**Figure 10.** The effect of treatment categories on fruit production in <u>single</u> inflorescence plants of *X. asphodeloides* at Orchid Hill in the 1998 and 1999 response years. Estimates are plotted against the first quartile, median, mean and third quartile values of the covariate on the abscissa. Bars indicate 95% confidence intervals. OF = open/fire treatment, SF = shaded/fire treatment. Maximum potential fruit production was calculated by assuming a 1:1 ratio of fruits/infructescence:flowers/inflorescence at the four covariate values.

Similar ANCOVA analyses on seed production produced similar results (**Table 3; Figure 11**). Once again, there was a highly significant effect of the covariate across all treatment categories, with larger inflorescences yielding progressively more seeds.

Despite producing fruits at the rate of 38-52% of the potential maximum, total seed production in control plants was only 16-22% of its maximum. In contrast, plants in the open/fire treatment produced approximately three times as many seeds, ranging from 52-63% of the maximum possible, and shaded/fire plants made twice as many seeds, yielding from 38-41% of the maximum. The covariate by treatment interaction was highly significant due to the much steeper slope of the open/fire category as compared with the control and shaded/fire categories. In this analysis the control and shaded/fire categories were grouped together because their slopes were parallel (i.e., not significantly different) to contrast against the OF treatment. As in the fruit production analysis, plants with small inflorescences in both fire treatment categories had essentially three times higher seed production than control individuals over all inflorescence sizes. Lastly, canopy opening with fire enhanced seed production in large inflorescences significantly more than in small inflorescences.

**Table 3.**  **A)**  Summary ANCOVA table for the effects of treatment (see also **Figure 11**) and isolation on seed production in 115 single inflorescence plants in the experimental response years of 1998 and 1999 at the Orchid Hill study site.  Total number of flowers/inflorescence (Totfl) was used as the covariate.  Control and shaded/fire treatments had parallel slopes and thus were grouped together (Group) to reduce the number of comparisons among treatment classes.  **B)**  Paired treatment comparisons for the significant covariate by treatment interaction (C = control, OF = open canopy/fire treatment, SF = shaded canopy/fire treatment; $\propto$ = 0.05).

**A)**                                Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Treatment | 2 | 107 | 7.30 | 0.0011 |
| Isolation | 1 | 107 | 0.22 | 0.6415 |
| Treatment*Isolation | 2 | 107 | 0.35 | 0.7074 |
| Totfl*Group | 2 | 107 | 60.71 | <.0001 |

**B)**

| Comparison | Estimate | Error | DF | t Value | Pr > |t| |
|---|---|---|---|---|---|
| OF-C at 25%=167 | 363.08 | 85.0795 | 107 | 4.27 | <.0001 |
| OF-C at 50%=206 | 477.79 | 76.6433 | 107 | 6.23 | <.0001 |
| OF-C at mean=221.4 | 523.03 | 75.7961 | 107 | 6.90 | <.0001 |
| OF-C 75%=270 | 666.04 | 82.8130 | 107 | 8.04 | <.0001 |
| OF-SF at 25%=167 | 112.84 | 70.5499 | 107 | 1.60 | 0.1127 |
| OF-SF at 50%=206 | 227.55 | 58.6313 | 107 | 3.88 | 0.0002 |
| OF-SF at mean=221.4 | 272.79 | 56.9152 | 107 | 4.79 | <.0001 |
| OF-SF at 75%=270 | 415.79 | 64.2938 | 107 | 6.47 | <.0001 |
| SF-C at mean=221.4 | 250.24 | 73.4754 | 107 | 3.41 | 0.0009 |
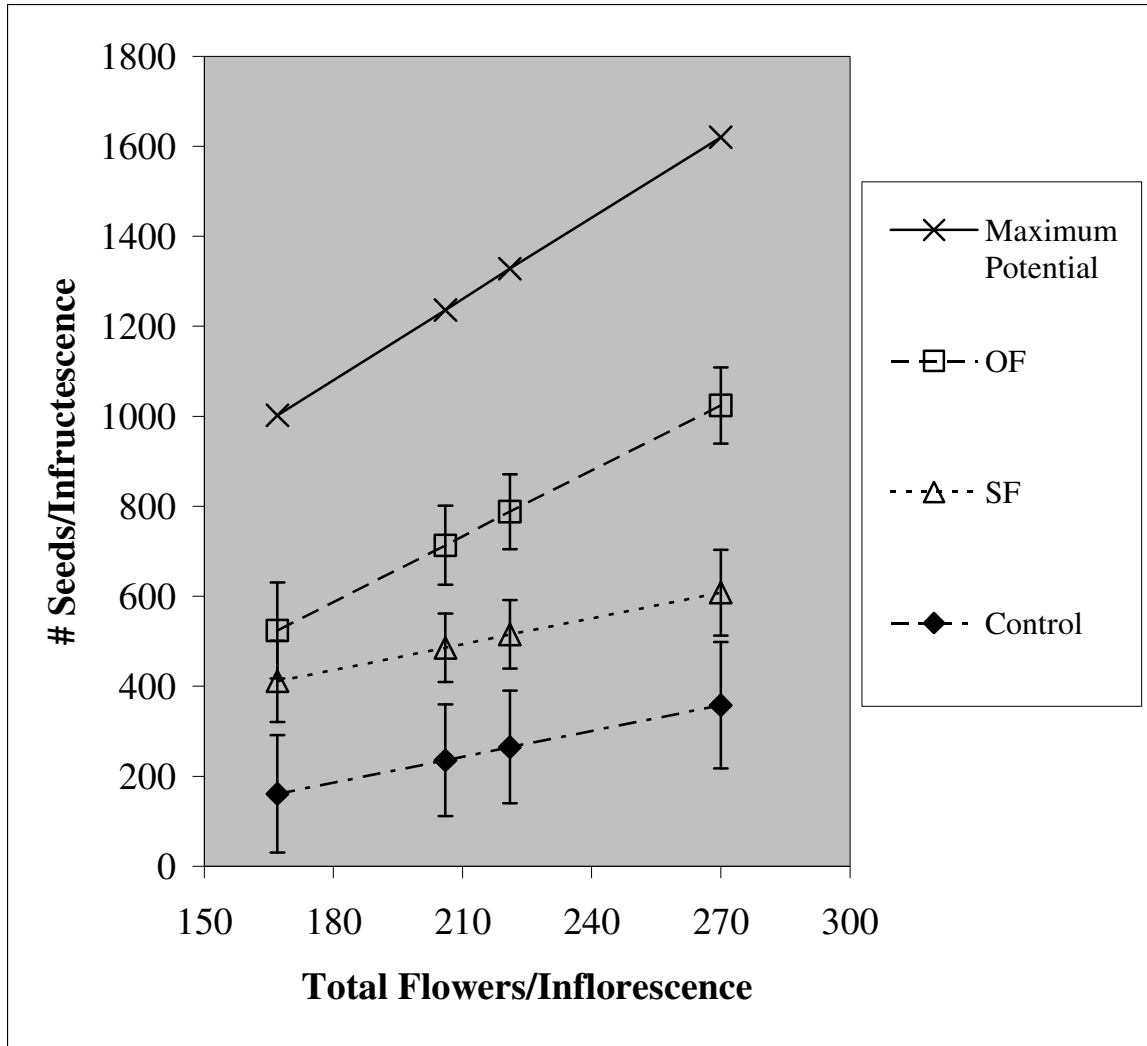
**Figure 11.** The effect of treatment categories on seed production in <u>single</u> inflorescence plants of *X. asphodeloides* at Orchid Hill in the 1998 and 1999 response years. Estimates are plotted against the first quartile, median, mean and third quartile values of the covariate on the abscissa. Bars indicate 95% confidence intervals. OF = open canopy/fire treatment, SF = shaded canopy/fire treatment. Maximum potential seed production was calculated by assuming a 1:1 ratio of fruits/infructescence:flowers/inflorescence at the covariate values and multiplying this number by six (the maximum number of seeds known to be produced per fruit).

Unexpectedly, detailed counts of seed yields from individual fruits of

infructescences collected in 1998 revealed that 55 infructescences from 28 plants bore

fruits that contained more than the maximum possible number of seeds based upon

previous floral anatomy studies (Utech 1978). Nearly all of these were produced in the

experimental treatments, with the open/fire strips containing 35 infructescences with 762 excess-seeded fruits and the shaded/fire strips harboring another 18 infructescences with 94 excess-seeded fruits. The control strip only had 2 infructescences that yielded a total of 10 excess-seeded fruits. Seed counts in these fruits ranged from 7-12/fruit, but the control plants never had more than seven seeds/fruit, while shaded/fire plants had some fruits that yielded as many as ten seeds and open/fire plants had fruits that regularly produced twelve seeds. The plants that produced the most excess-seeded fruits/infructescence were open/fire treatment plants with two or more flower stalks.

Evaluation of fruit and seed set in the 2000 season at Orchid Hill gave indication of the poor reproductive performance of plants in years of low flowering. A total of only 7 flower stalks were produced among six plants in that year, consisting of one double-stalked plant in the control strip, three single-stalked plants in the open/fire strips, and two single-stalked plants in the shaded/fire strips. Due to this low sample size, these data could not be analyzed with an ANCOVA. However, the arithmetic means and standard deviations for fruit and seed set of these seven stalks were $93.43 \pm 80.3$ and $15.43 \pm 33.0$ respectively. Both values were very low, particularly seed set, despite the fact that four of the six plants had not participated in the 1998 and 1999 mass-flowering response years, either never flowering during the fifteen year monitoring period or not flowering since before 1996.

Comparison of the reproductive performance of the Orchid Hill control plants with two other nearby undisturbed, shaded turkeybeard populations in 1998 and 1999

showed a significant effect of the inflorescence size covariate for both fruit production

(**Table 4**) and seed production (**Table 5; Figure 12**), similar to the previous analyses.

There was no significant difference in fruit production among the three populations

(**Table 4**), although they did differ in terms of seed production due to significantly lower

yields from plants in the BMK2 population (**Table 5; Figure 12**).  The regressions of

seed production as a function of the covariate inflorescence size for the OH and LRB

populations did not differ significantly from each other in slope or elevation ($t_{(1, 42.8)} =$

1.73, p = 0.09; **Table 5**).  Reproductive performance in the control plants at the Orchid

Hill study site was therefore equivalent, falling in the middle of the range of undisturbed

turkeybeard plants flowering at the same time in other local populations.


**Table 4.**  Summary ANCOVA table for the effects of population and isolation on fruit
production in 54 single inflorescence plants for the control plants at Orchid Hill (OH) and
two nearby undisturbed *X. asphodeloides* populations at the Long Run Bottom (LRB) and
Benchmark2 (BMK2) sites in 1998 and 1999.  Total number of flowers/inflorescence
(Totfl) was used as the covariate.

Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Population | 2 | 34.8 | 1.25 | 0.2977 |
| Isolation | 1 | 31.3 | 2.03 | 0.1637 |
| Population*Isolation | 2 | 41.9 | 2.78 | 0.0735 |
| Totfl | 1 | 19.8 | 27.04 | <.0001 |

**Table 5. A)** Summary ANCOVA table for the effects of population and isolation (see also **Figures 12 and 13**) on seed production in 54 single inflorescence plants for the control plants at Orchid Hill (OH) and two nearby undisturbed *X. asphodeloides* populations at the Long Run Bottom (LRB) and Benchmark2 (BMK2) sites in 1998 and 1999. Total number of flowers/inflorescence (Totfl) was used as the covariate. The LRB and OH populations had parallel slopes and thus were grouped together (Group) to reduce the number of comparisons among populations. **B)** Paired population comparisons for the significant covariate by population interaction ($\propto = 0.05$). Data were square root transformed to meet ANCOVA assumptions, and estimated differences are the back-transformed values.

**A)**                      Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| Population | 2 | 40.9 | 4.59 | 0.0159 |
| Isolation | 1 | 40.3 | 0.42 | 0.5216 |
| Population*Isolation | 2 | 42.5 | 6.63 | 0.0031 |
| Totfl*Group | 2 | 39.1 | 26.04 | <.0001 |

**B)**

| Comparison | Estimate | Error | DF | t Value | Pr > |t| |
|---|---|---|---|---|---|
| LRB-BMK2 at 25%=143 | 2.30 | 8.7202 | 44.5 | 0.51 | 0.6101 |
| LRB-BMK2 at 50%=192 | 23.06 | 6.0059 | 45.7 | 1.96 | 0.0562 |
| LRB-BMK2 at mean=198.1 | 27.12 | 5.8685 | 45.7 | 2.15 | 0.0369 |
| LRB-BMK2 at 75%=245 | 69.81 | 6.2871 | 45.1 | 3.33 | 0.0017 |
| OH-BMK2 at 25%=143 | -6.61 | 4.5233 | 40.1 | -1.21 | 0.2338 |
| OH-BMK2 at 50%=192 | 0.51 | 2.7692 | 38.0 | 0.43 | 0.6701 |
| OH-BMK2 at mean=198.1 | 1.26 | 2.7510 | 37.5 | 0.68 | 0.5033 |
| OH-BMK2 at 75%=245 | 18.22 | 4.0889 | 35.1 | 2.11 | 0.0420 |
| LRB-OH at mean=198.1 | 16.71 | 5.5998 | 42.8 | 1.73 | 0.0913 |
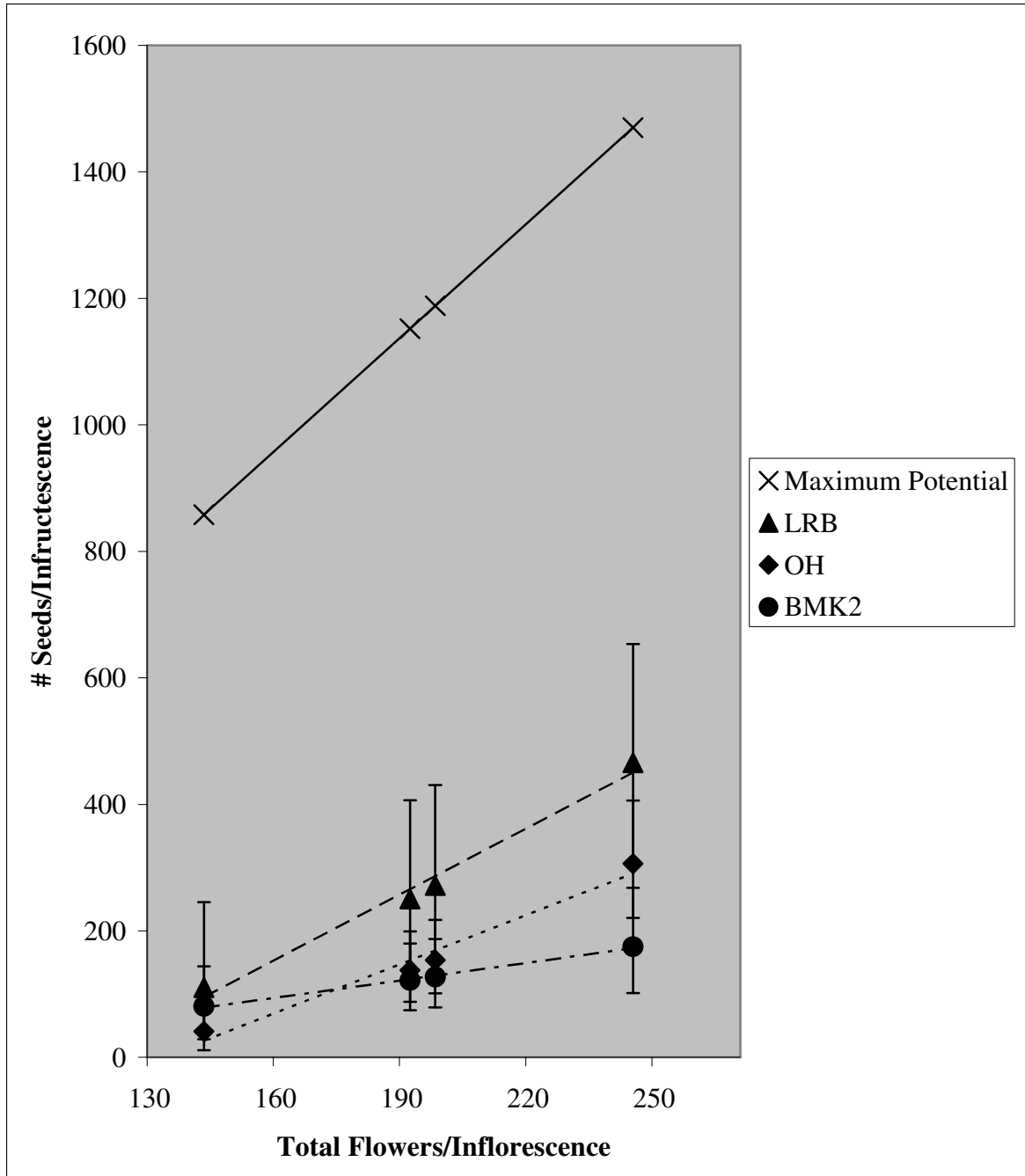
**Figure 12.** Comparison of seed production per inflorescence in Orchid Hill (OH) control plants with plants from two nearby undisturbed, shaded populations, Long Run Bottom (LRB) and Benchmark2 (BMK2), in 1998 and 1999. Estimates are back-transformed values and are plotted against the first quartile, median, mean and third quartile values of the covariate on the abscissa. Bars indicate 95% confidence intervals. Maximum potential seed production was calculated by assuming a 1:1 ratio of fruits/infructescence:flowers/inflorescence at the covariate values and multiplying this number by six (the maximum number of seeds known to be produced per fruit).

*3. Flowering plant density - habitat manipulation experiment:*

The factor of flowering plant density was included as a second main effect in the ANCOVA analyses of fruit and seed production in single inflorescence plants at Orchid Hill.  There was no significant effect of relative isolation of flowering plants on fruit or seed production in these analyses (**Tables 2 and 3**), although plants that were relatively more isolated from other flowering plants had slightly higher average levels of fruit and seed set than those more clumped together with other flowering individuals.  In the comparison of undisturbed populations with Orchid Hill controls there was a significant population by isolation interaction effect on seed production (**Table 5**), with inflorescences from clumped plants in the BMK2 population producing significantly more seeds than those of isolated plants, while plants in the LRB and OH populations showed the opposite pattern (**Figure 13**).
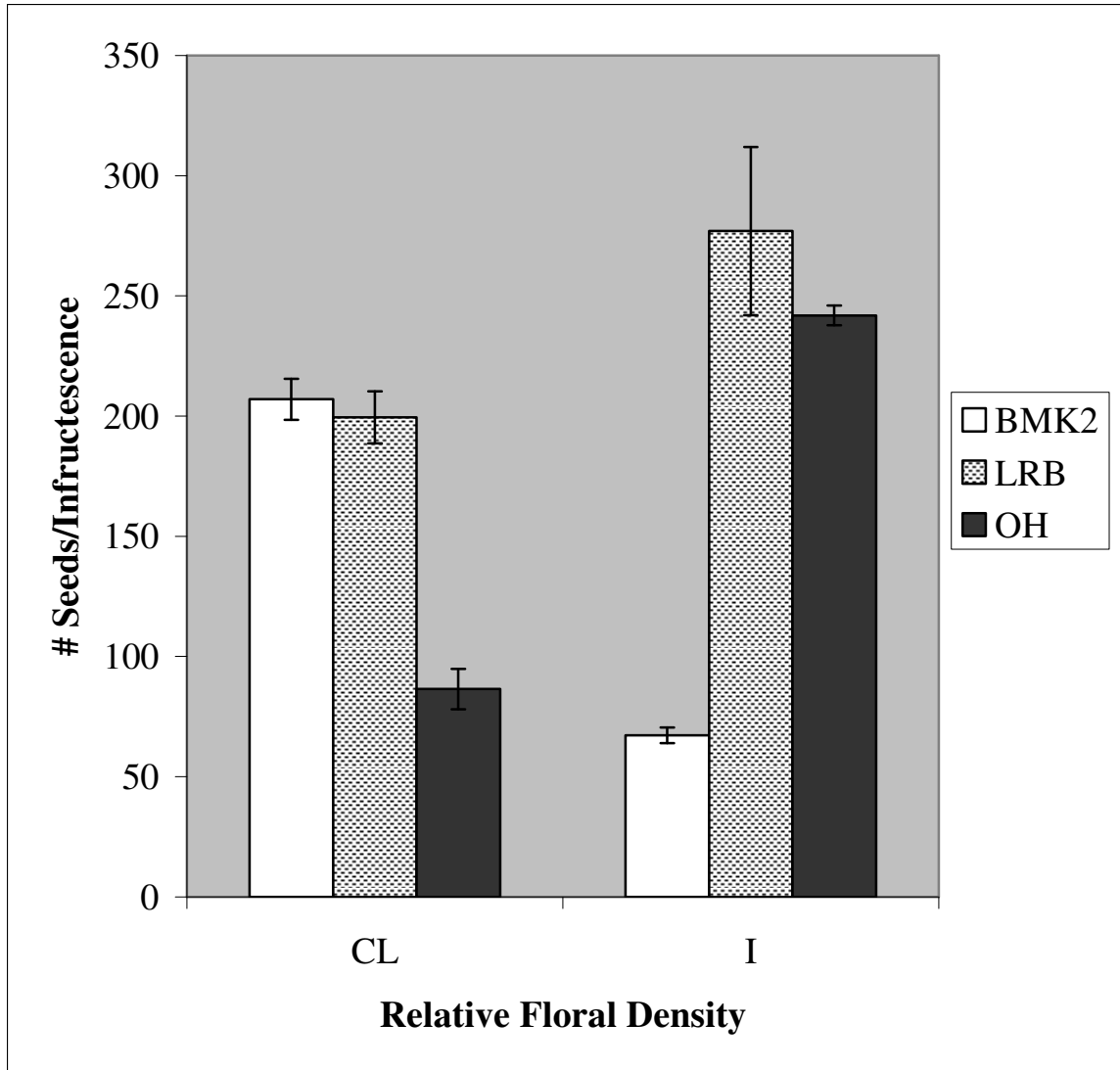
**Figure 13.** Population by isolation interaction in seed production per inflorescence ($F_{(2, 42.5)}$ = 6.63, p = 0.003; n = 54) for Orchid Hill (OH) control plants and plants from two nearby undisturbed, shaded populations, Long Run Bottom (LRB) and Benchmark2 (BMK2), in 1998 and 1999. Relative floral density was divided into two categories: inflorescences occurring in clumps with other flowering plants (CL) and inflorescences isolated from other flowering plants (I). Least squares mean estimates are back-transformed values; bars represent $\pm$ 2 standard errors.

*4. Number of flowering stalks (inflorescences) - habitat manipulation*

*experiment:*

A highly significant effect of the covariate of inflorescence size was maintained in the ANOVA analyses of fruit production in 266 inflorescences from 140 plants (**Table 6; Figure 14**).  Overall the main effect of flower stalk number on fruit production/inflorescence was marginally significant ($F_{(4, 229)}$ = 2.41, p = 0.0499, n = 266); however, it was those plants having five or more flowering stalks that were largely responsible for this as well as the significant covariate by stalk number interaction.  Inflorescences from such plants yielded significantly fewer fruits/inflorescence on average than those coming from plants with fewer flower stalks, except at the lowest values of the covariate (**Table 6**).  Inflorescences from plants with two flower stalks produced the most fruits per inflorescence, followed by those with three, one and four flowering stalks.  Significant differences among these four categories occurred only between the 2-stalked plants and those bearing four stalks, with the former producing significantly more fruits.

**Table 6. A)** Summary ANCOVA table for the effects of number of flowering stalks (Numstalks) (see also **Figure 14**) and treatment on fruit production in 266 inflorescences from 140 plants in the experimental response years of 1998 and 1999 at the Orchid Hill study site. Total number of flowers/inflorescence (Totfl) was used as the covariate. The single-, double-, triple- and quadruple-stalked categories had parallel slopes and thus were grouped together (Group) to reduce the number of comparisons among flower stalk number classes. **B)** Paired stalk number comparisons for the significant covariate by number of flowering stalks interaction ($\propto = 0.05$). S = single-stalked plants, D = double-stalked plants, T = triple-stalked plants, Q = quadruple-stalked plants, and M = $\geq$5-stalked plants.

**A)** Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| NumStalks | 4 | 229 | 2.41 | 0.0499 |
| Treatment | 1 | 232 | 1.86 | 0.1739 |
| NumStalks*Treatment | 4 | 231 | 0.78 | 0.5416 |
| Totfl*Group | 2 | 246 | 129.61 | <.0001 |

**B)**

| Comparison | Estimate | Error | DF | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| D-M at 25%=158 | 24.2960 | 12.9285 | 228 | 1.88 | 0.0615 |
| D-M at 50%=203.5 | 40.9784 | 11.7934 | 226 | 3.47 | 0.0006 |
| D-M at mean=221.4 | 47.5413 | 11.9093 | 227 | 3.99 | <.0001 |
| D-M at 75%=273 | 66.4602 | 13.9040 | 230 | 4.78 | <.0001 |
| T-M at 25%=158 | 15.1713 | 14.9466 | 230 | 1.02 | 0.3112 |
| T-M at 50%=203.5 | 31.8537 | 13.6289 | 227 | 2.34 | 0.0203 |
| T-M at mean=221.4 | 38.4166 | 13.5913 | 226 | 2.83 | 0.0051 |
| T-M at 75%=273 | 57.3355 | 15.0112 | 227 | 3.82 | 0.0002 |
| S-M at 25%=158 | 7.2282 | 10.3052 | 228 | 0.70 | 0.4838 |
| S-M at 50%=203.5 | 23.9105 | 8.9380 | 230 | 2.68 | 0.0080 |
| S-M at mean=221.4 | 30.4734 | 9.1283 | 232 | 3.34 | 0.0010 |
| S-M at 75%=273 | 49.3923 | 11.6963 | 237 | 4.22 | <.0001 |
| Q-M at 25%=158 | -5.5376 | 12.9301 | 228 | -0.43 | 0.6689 |
| Q-M at 50%=203.5 | 11.1448 | 12.1313 | 230 | 0.92 | 0.3592 |
| Q-M at mean=221.4 | 17.7077 | 12.3726 | 232 | 1.43 | 0.1537 |
| Q-M at 75%=273 | 36.6266 | 14.6182 | 236 | 2.51 | 0.0129 |
| D-T at mean=221.4 | 9.1247 | 15.3172 | 227 | 0.60 | 0.5520 |
| D-S at mean=221.4 | 17.0679 | 11.3362 | 223 | 1.51 | 0.1336 |
| D-Q at mean=221.4 | 29.8336 | 14.1640 | 228 | 2.11 | 0.0363 |
| T-S at mean=221.4 | 7.9432 | 13.3600 | 232 | 0.59 | 0.5527 |
| T-Q at mean=221.4 | 20.7089 | 15.7046 | 229 | 1.32 | 0.1886 |
| S-Q at mean=221.4 | 12.7657 | 11.7941 | 228 | 1.08 | 0.2802 |
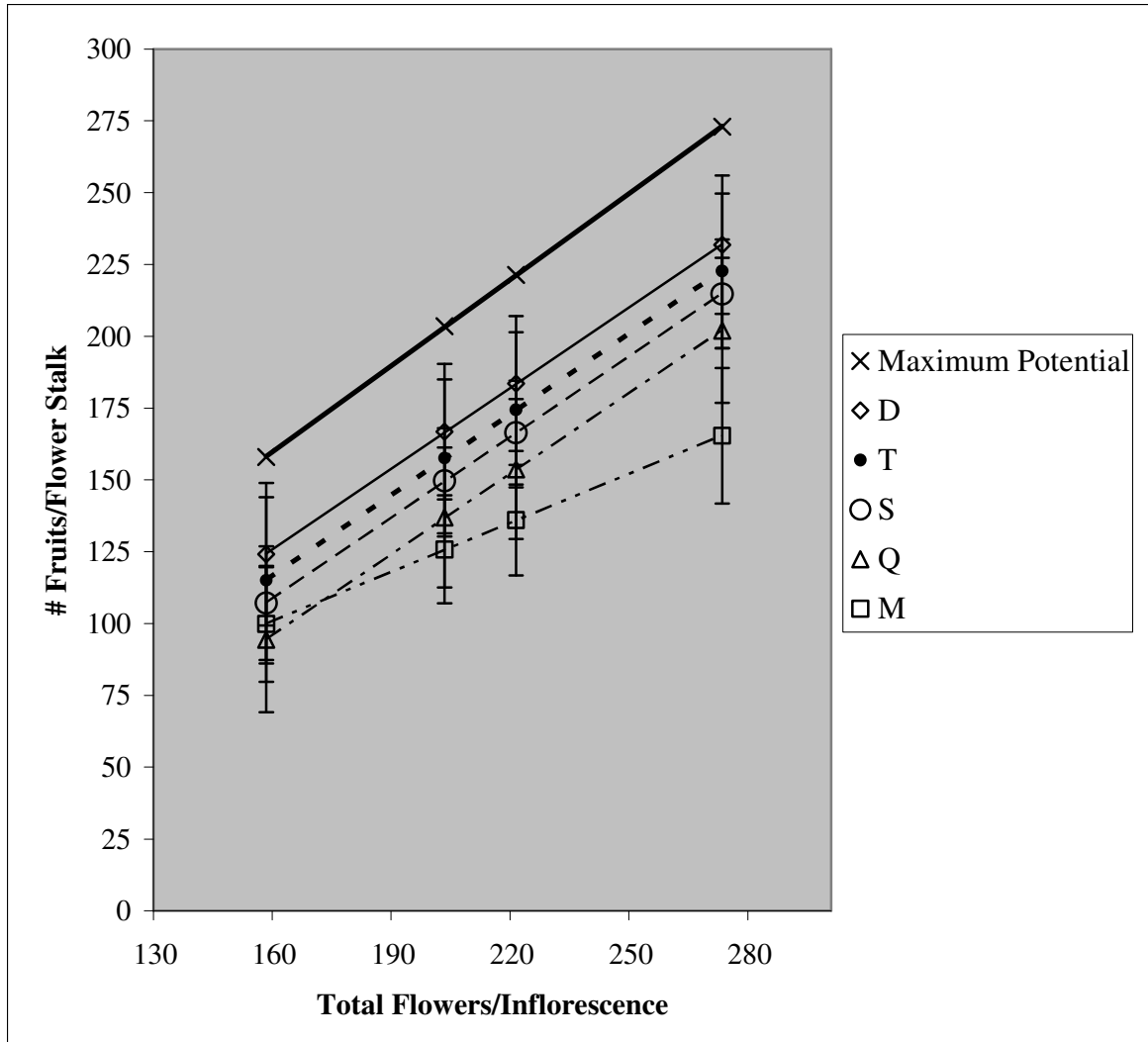
**Figure 14.** The effect of flower stalk number on fruit production in *X. asphodeloides* at Orchid Hill in the 1998 and 1999 response years. Estimates are plotted against the first quartile, median, mean, and third quartile values of the covariate on the abscissa. Bars indicate 95% confidence intervals. S = single-stalked plants, D = double-stalked plants, T = triple-stalked plants, Q = quadruple-stalked plants, and M = ≥5-stalked plants. Maximum potential fruit production was calculated by assuming a 1:1 ratio of fruits/infructescence:flowers/inflorescence at the four covariate values.

Similar results were obtained in the ANCOVA analyses of seed production, except that the effect of flower stalk number per plant on seed yield per inflorescence was much greater ($F_{(4, 236)}$ = 5.36, p = 0.0004, n = 266; **Table 7; Figure 15**). Once again, this was due mainly to the plants with ≥ 5 stalks, which produced similar numbers of seeds

regardless of inflorescence size (i.e., across all values of the covariate), whereas plants in the other flower stalk categories followed the typical pattern of higher seed production with increasing inflorescence size. Two-stalked plants had the highest per inflorescence seed production, followed by nearly identical seed yields in 1- and 3-stalked individuals and then lower levels in 4-stalked plants. Once again, among these four categories only 2-stalked plants achieved significantly higher seed yield over 4-stalked individuals. Notably, examination of total seed production per plant showed that all multiple stalk categories had substantially higher per plant yields than that of single-stalked individuals (**Figure 16**), even though plants with five or more stalks exhibited the lowest and most similar seed production on a per stalk basis.

**Table 7.** **A)** Summary ANCOVA table for the effects of number of flowering stalks (Numstalks) (see also **Figure 15**) and treatment on seed production in 266 inflorescences from 140 plants in the experimental response years of 1998 and 1999 at the Orchid Hill study site. Total number of flowers/inflorescence (Totfl) was used as the covariate. The single-, double-, triple- and quadruple-stalked categories had parallel slopes and thus were grouped together (Group) to reduce the number of comparisons among flower stalk number classes. **B)** Paired stalk number comparisons for the significant covariate by number of flowering stalks interaction ($\alpha = 0.05$). See Table 6 for definitions of stalk number category abbreviations. **C)** Least squares means for the significant treatment main effect (OF = open canopy/fire treatment, SF = shaded canopy/fire treatment).

**A)**

Type 3 Tests of Fixed Effects

| Effect | Num DF | Den DF | F Value | Pr > F |
|---|---|---|---|---|
| NumStalks | 4 | 236 | 5.36 | 0.0004 |
| Treatment | 1 | 242 | 13.69 | 0.0003 |
| NumStalks*Treatment | 4 | 240 | 2.17 | 0.0736 |
| Totfl*Group | 2 | 253 | 65.78 | <.0001 |

**B)**

| Comparison | Estimate | Error | DF | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| D-M at 25%=158 | 12.72 | 80.3765 | 234 | 0.16 | 0.8744 |
| D-M at 50%=203.5 | 155.79 | 73.5091 | 229 | 2.12 | 0.0351 |
| D-M at mean=221.4 | 212.08 | 74.2115 | 230 | 2.86 | 0.0047 |
| D-M at 75%=273 | 374.33 | 86.3027 | 236 | 4.34 | <.0001 |
| T-M at 25%=158 | -80.58 | 92.7340 | 237 | -0.87 | 0.3858 |
| T-M at 50%=203.5 | 62.50 | 84.8721 | 232 | 0.74 | 0.4623 |
| T-M at mean=221.4 | 118.78 | 84.6963 | 230 | 1.40 | 0.1621 |
| T-M at 75%=273 | 281.03 | 93.4304 | 233 | 3.01 | 0.0029 |
| S-M at 25%=158 | -76.50 | 64.0825 | 234 | -1.19 | 0.2338 |
| S-M at 50%=203.5 | 66.57 | 55.5070 | 235 | 1.20 | 0.2316 |
| S-M at mean=221.4 | 122.86 | 56.5429 | 238 | 2.17 | 0.0308 |
| S-M at 75%=273 | 285.11 | 71.9261 | 247 | 3.96 | <.0001 |
| Q-M at 25%=158 | -187.33 | 80.4092 | 234 | -2.33 | 0.0207 |
| Q-M at 50%=203.5 | -44.26 | 75.2645 | 237 | -0.59 | 0.5571 |
| Q-M at mean=221.4 | 12.03 | 76.6107 | 239 | 0.16 | 0.8754 |
| Q-M at 75%=273 | 174.28 | 90.0013 | 246 | 1.94 | 0.0540 |
| D-T at mean=221.4 | 93.30 | 95.3837 | 231 | 0.98 | 0.3290 |
| D-S at mean=221.4 | 89.22 | 70.8698 | 225 | 1.26 | 0.2094 |
| D-Q at mean=221.4 | 200.05 | 88.1030 | 233 | 2.27 | 0.0241 |
| T-S at mean=221.4 | 4.07 | 82.7026 | 240 | 0.05 | 0.9608 |
| T-Q at mean=221.4 | 106.76 | 97.5685 | 235 | 1.09 | 0.2750 |
| S-Q at mean=221.4 | 110.83 | 73.3648 | 233 | 1.51 | 0.1322 |

**C)**

| Treatment | Estimate | Error | DF | t Value | Pr > \|t\| |
|---|---|---|---|---|---|
| OF | 722.42 | 45.1142 | 74.6 | 16.01 | <.0001 |
| SF | 538.57 | 46.7276 | 85.5 | 11.53 | <.0001 |
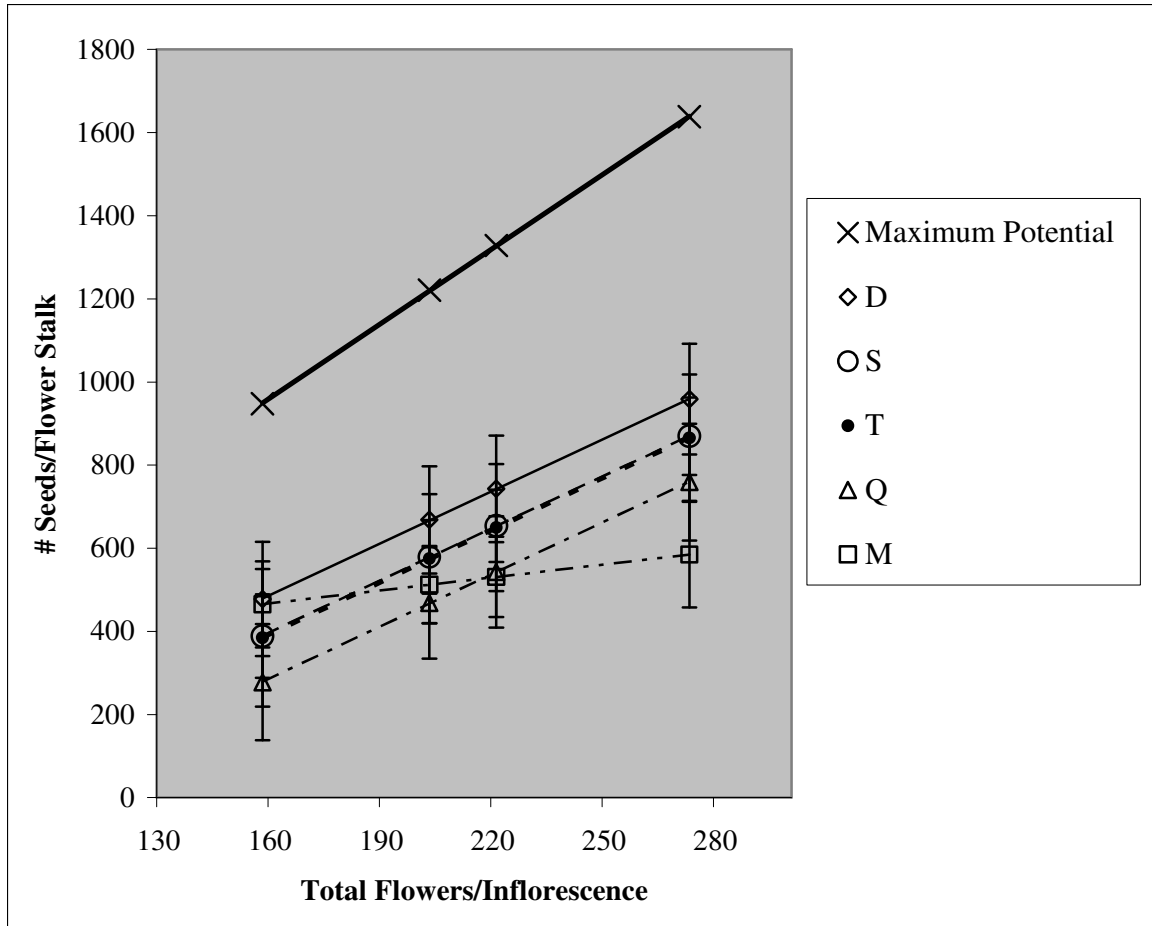
**Figure 15.** The effect of flower stalk number on seed production in *X. asphodeloides* at Orchid Hill in the 1998 and 1999 response years. Estimates are plotted against the first quartile, median, mean and third quartile values of the covariate on the abscissa. Bars indicate 95% confidence intervals. S = single-stalked plants, D = double-stalked plants, T = triple-stalked plants, Q = quadruple-stalked plants, and M = ≥5-stalked plants. Maximum potential seed production was calculated by assuming a 1:1 ratio of fruits/infructescence:flowers/inflorescence at the covariate values and multiplying this number by six (the maximum number of seeds known to be produced per fruit).
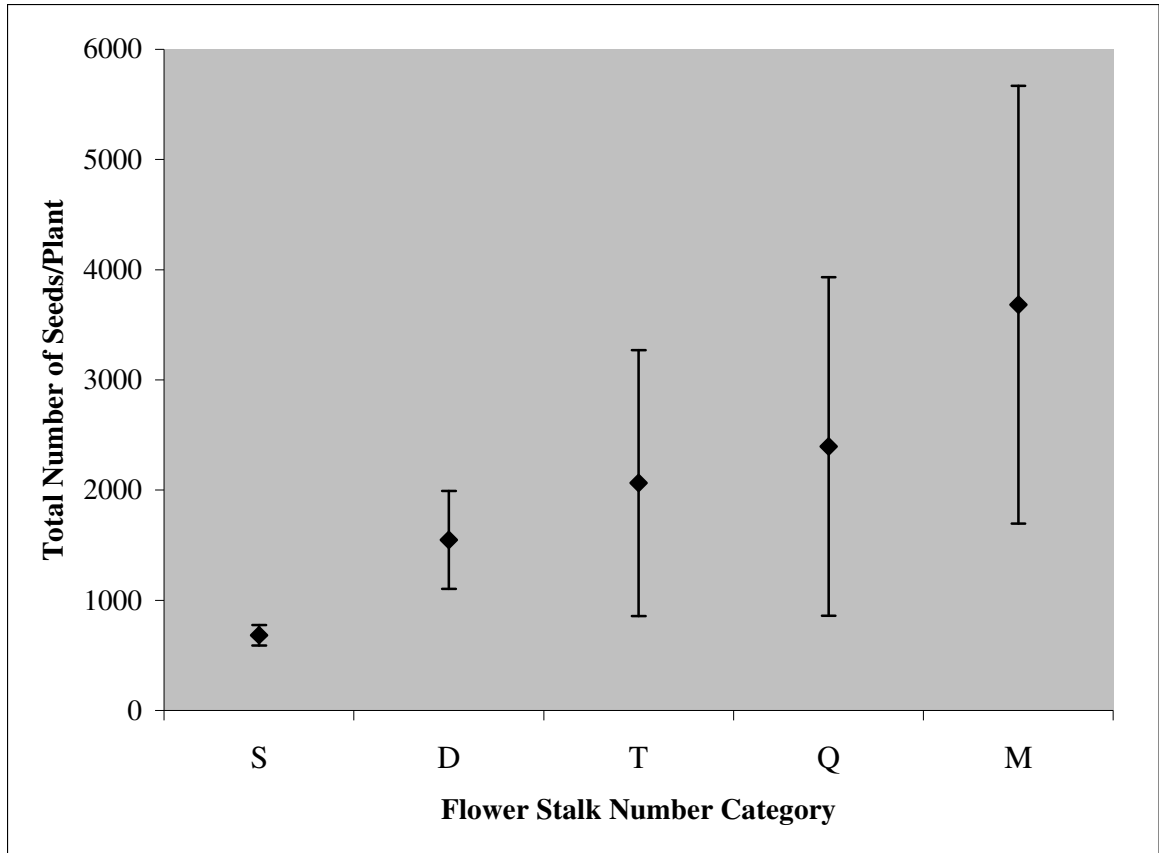
**Figure 16.** Total seed production per plant for the five flowering stalk categories used in the analyses of the effect of multiple flower stalks on reproductive performance at Orchid Hill in the 1998 and 1999 response years. Bars indicate 95% confidence intervals. S = single-stalked plants, D = double-stalked plants, T = triple-stalked plants, Q = quadruple-stalked plants, and M = $\geq$5-stalked plants.

The main effect of treatment was included again in the ANCOVAs of flower stalk number effect on fruit and seed production to test for differences between open/fire and shaded/fire treated plants only, because no control plants were included here since multiple stalk production did not occur in the control quadrats. No significant effect on fruit production was found between these two treatment categories(**Table 6**) but there was a significant effect on seed production, with open/fire treated plants producing significantly more seeds than shaded/fire treated plants (**Table 7**). This result was in

accordance with the earlier analysis of treatment effects on single inflorescence plants presented in Table 3.

Fire history of turkeybeard populations:

Evaluation of fire-scarred tree cross-sections taken from the Orchid Hill site and six other sites on the GWNF harboring *X. asphodeloides* populations revealed substantial evidence of repeated past fires at most locations over the past 200+ years, although the number of sampled trees per site was small (**Table 8**). Trees from Orchid Hill showed scars from six chronologically distinct fires over a 125 – year period, with four of these occurring pre-1940, which was the year that the U.S. Forest Service's policy of suppression of wildfires went into full effect on the GWNF (USDA 1993, USFS 1997, S. Croy 2003, pers. comm.). As a consequence, the pre-1940 mean fire interval at Orchid Hill was 12.7 years. All but one of the other six sites experienced at least two historical fires, with one site, Black Run, having eight fires over the past 216 years, seven of which occurred pre-1940. Mean pre-1940 fire intervals ranged between 9.0 and 18.2 years at these additional sites.

**Table 8.** Fire histories of turkeybeard population sites on the Dry River Ranger District, GWNF, VA, obtained from cross-sectional annual growth ring analysis of fire-scarred trees.

| Site | No. of sampled trees | Age of oldest sampled tree (years) | Total No. of fires | No. of fires pre-1940 | Mean fire interval pre-1940 (years $\pm$ 1 SD) |
|---|---|---|---|---|---|
| Benchmark 2 | 3 | 106+ | 1 | 1 | N/A |
| Black Run | 5 | 216 | 8 | 7 | 18.2 $\pm$ 10.4 |
| Dyers Knob | 4 | 114 | 3 | 2 | N/A |
| Feedstone Mtn. | 4 | 165+ | 2 | 1 | N/A |
| Hone Quarry | 5 | 120 | 3 | 3 | 9.0 $\pm$ 0.0 |
| Orchid Hill | 10 | 125 | 6 | 4 | 12.7 $\pm$ 11.0 |
| Rocky Run | 5 | 190 | 4 | 4 | 14.3 $\pm$ 4.2 |

**Discussion:**

This study represents one of the most extensive documentations of the ecology of a fire-adapted forest understory plant species in the Appalachians to date. Bond and van Wilgen (1996) stated that one of the best indicators of an adaptive response to fire is fire-stimulated reproduction, which this study has documented convincingly for *X. asphodeloides*.

The depletion curves of the adult and seedling cohorts of *X. asphodeloides* (**Figure 5**) were typical Type III in form (Pearl 1928), with high mortality in the early seedling years followed by a long and stable adult period. Importantly, although there was high mortality in the second mass-flowering season of 1999 it is unlikely that this could be attributed to either a cost of reproduction or to the fire and canopy opening

treatments because it happened across all four cohorts.  It seems more probable that it

was related to the fact that 1999 was a severe drought year throughout Virginia.

Contrary to some claims of monocarpy (Takhtajan 1997), most individual plants of

turkeybeard did not die after flowering, especially in both 1998 and 1999.  The adult

median life expectancy of 49 years implies that plants could have experienced one to

several fires during their lifetime under the historical fire regime range estimated from

fire scar analysis (**Table 8**) and found in previous dendrochronological studies in this

portion of the Appalachians (Harmon 1982, Sutherland et al. 1993, Williams 1998,

Harrod et al. 2000, Shumway et al. 2001).  Fire occurrences in turkeybeard habitat post-

1940 (i.e., under current federal fire suppression practices) were likely too infrequent,

however, for the average individual to have taken advantage of a post-burn reproductive

environment.


Despite the recording of the first major seedling germination and establishment

event in the open/fire strips in 1997, substantial numbers of seedlings also established in

the control strip the following year.  Nevertheless, fire-stimulated germination cannot be

ruled out in this case because heavy smoke was produced by the 1996 prescribed fire and

the control quadrats were highly exposed to it due to the prevailing wind direction during

the burn and their position immediately upslope from the experimental strips.  Ethylene-,

charred wood-, and most recently smoke-stimulated seed germination has been described

for both dicots and some species of liliaceous monocots on at least three continents (Gill

and Ingwersen 1976, Keeley and Pizzorno 1986, Keeley 1993, Keeley and Fotheringham

1997, 1998).  Further work is therefore required to elucidate germination requirements

for *X. asphodeloides* including the role, if any, that fire might play.  In addition,

herbivory on turkeybeard inflorescences by white-tailed deer had a minor impact in most

populations, but the extremely high levels found at the Feedstone Mountain site showed

the negative effect that elevated deer densities could have on reproduction in *X.*

*asphodeloides*.  Although this population is located on the GWNF, it borders a large

private hunt club inholding where supplemental feeding of deer has been a long-standing

practice.  This was likely responsible for the signs of high deer numbers observed at the

site.  Deer densities in the vicinity of turkeybeard sites should thus be taken into

consideration if burning is being planned as a management tool to enhance flowering.


The generally large spatial extents and population sizes estimated during the line

transect surveys of turkeybeard sites (**Table 1**) beg the question of how such populations

established and maintained themselves given that *X. asphodeloides* is a nonclonal, largely

self-incompatible (Bourg in prep.) and infrequently flowering species.  Eighty percent

(20 of 25) of these populations were at least one hectare in extent, with seven being at

least ten hectares.  Four sites had densities of at least 1 plant/m$^2$ and population sizes

reached at least 100,000 at six sites.  The findings of this study strongly point toward

recurrent past fire and its associated canopy alteration as the agents that stimulated the

mass reproduction seemingly necessary for creating such large occurrences of *X.*

*asphodeloides*.  As an example of the type of reproduction that could happen in a large

population following fire, the line transect data from the Rip Rap site in 2002 indicated

that approximately 31,000 individuals flowered.  Given the fact that this took place under

totally open canopy conditions similar to the open/fire strips at Orchid Hill, many

millions of seeds were laid down at the Rip Rap site in that year. It is plausible that once a hypothetical turkeybeard population became established, the combination of individual longevity, mass reproduction, and sufficiently short fire intervals could have lead to population expansion and even possibly the creation and self-perpetuation of a fire-adapted plant community, as first suggested by Mutch (1970). The Mutch hypothesis argued that fire-prone vegetation has evolved characteristics that increase flammability, thereby contributing to the perpetuation of fire-dependent communities such as pine-dominated habitats in otherwise mixed pine-oak forest types (Williamson and Black 1981, Rebertus et al. 1989). Although his hypothesis was flawed due to its entanglement with group selectionist logic, Bond and Midgley (1995) and Bond and van Wilgen (1996) rephrased it in terms of individualistic selection on traits that could enhance flammability such as fine, scleromorphic leaves (Rundel 1981, Papio and Trabaud 1991), which are possessed in abundance by *X. asphodeloides*. The high densities seen in many turkeybeard populations provide an ideal fine fuels layer for the spread of fire across the forest floor and into the shrub and canopy tree layers, and the capacity for rapid resprouting in turn by this species enables quick reestablishment of this fuel source. Notably, Ashman et al. (2004) also raised the question of whether plants evolve traits when subjected to environmental disturbances in the context of their effect on pollinator limitation, which also has relevance for *X. asphodeloides*.

*The Fire/Canopy Alteration Effect Hypothesis:*

In the context of the long-term flowering data (**Figure 7**), the impact of the experimental fire treatment dramatically demonstrated a significant positive effect of fire on inflorescence production for the following two reasons. First, evidence for a fire effect can be seen by comparing the flowering in the shaded/fire strips in 1998 and 1999 with the 1992-1995 flowering data in the same shaded strips without fire. These data show that the large fire effect here occurred mainly in 1999, the third post-fire year, when inflorescence production in the shaded/fire strips was particularly high. Second, the slightly elevated pre-experiment flowering years of 1993 and 1994 likely occurred as a lagged response to the gypsy moth-induced canopy opening in 1990-1991, which occurred in the absence of fire. The striking difference between the pre-experimental (1990-1994) flowering data and the large responses in the open canopy/fire strips in 1998 and 1999 thus represents a fire effect also, because the open canopy factor was only a partial contributor to the huge mass flowering witnessed after the prescribed fire treatment. Further support for this assertion of dual contributory effects of fire and canopy removal comes from the Rip Rap and Hone Quarry Ridge turkeybeard populations, which burnt in separate fires in April 1999. The large mass flowering responses witnessed in these populations also occurred in the second and third post-burn years under conditions of complete canopy removal, as both sites had experienced stand-replacing fire, with the added impact of heavy pre-burn fuel loading due to southern pine beetle (*Dendroctonus frontalis*) outbreak at the Rip Rap site (Nicholas and White 1984, Raeburn 2002 pers. comm.). Overall therefore, fire interacted with canopy opening to

some extent to yield lagged mass-flowering in *X. asphodeloides* in the second and third post-disturbance years, while treatment with fire alone produced mass-flowering predominantly in the third post-disturbance year.  The experiment did not permit evaluation of any effect of seasonality of burning on mass reproduction.  The prescribed fire at Orchid Hill as well as the other known wildfire occurrences in neighboring turkeybeard populations all occurred in the month of April during the study period. Historically, wildfires in this portion of the Appalachians were most common in the spring (USFS 1997), thus supporting the contention that the observed flowering effects were representative of those that would have occurred under the natural fire regime for the region.

The fire response of turkeybeard contrasted markedly with the response of the pink lady's-slipper orchid (*Cypripedium acaule*), another long-lived perennial present in abundance at Orchid Hill and from which the site name is derived.  Long-term monitoring studies conducted from 1977 - present on more than 6,000 marked individuals in this population showed definitively that *C. acaule* is a canopy gap responder, because it mass-flowered and fruited only in the open/fire treatment strips in response to the fire/canopy alteration experiment (Gill 1996, Gill unpublished data).  Flowering and fruit set in the shaded/fire strips were no different than the low flowering levels recorded in pre-experiment years for this species.  Additionally, canopy gap-induced germination and flowering was documented in the open/fire strips for sneezeweed or fireweed (*Erechtites hieracifolia*; Asteraceae), an annual that appeared from the seed bank in great abundance for the first time in the summer 1996 post-fire growing season (Bennett, Gill and Bourg

60

unpublished data).  Although the consumption of the duff layer by the fire may have been

a factor in creating the proper germination conditions, this species did not respond in the

shaded/fire strips either.  The response of *X. asphodeloides* in these same shaded/fire

strips was thus of a distinctly different nature than that of other notable herbaceous

species that exhibited increased reproduction due to the experimental manipulations at

the site.  Such highly individualistic responses of different species to burning are a

common feature of fire-influenced plant communities (Bond and van Wilgen 1996).


The patterns of flowering frequency and intervals were also dominated by the

responses of the 1998 and 1999 seasons, which could be attributed only to the habitat

alteration caused by the canopy removal and burning treatments.  More than one third of

all the mature plants in the marked population that had ever reproduced did so for their

first time during these two years (**Figure 8**).  Additionally, upon casual inspection of the

flowering interval data (**Figure 9**) plants appeared to exhibit a substantial tendency to

flower in two consecutive years (i.e., the 1-year interval category) before entering a non-

flowering period.  However, many of these were individuals that flowered in both 1998

and 1999, and only 30% of all the plants in the 1-year interval category exhibited an

ability to repeat this particular flowering periodicity.  The low levels of flowering interval

repetition in this *X. asphodeloides* population offer no support for any claims of a

periodic or cyclic nature to reproduction, despite long-standing anecdotal accounts of

septenniality (7-year cycles) in the congeneric *X. tenax* (Eastwood 1898, Jepson 1901).

Indeed, Eastwood (1898) also relates the accounts of four other observers of various *X.*

*tenax* populations in northern California, two of which claimed a cycle of two successive

flowering seasons, another a cycle of five years, and the last a pattern of annual blooming. Based on the empirical and experimental patterns exhibited at Orchid Hill and at the other burned populations surveyed on the GWNF and SNP, it appears much more plausible that large population-level flowering events in *Xerophyllum* are induced by prior recent disturbance, such as fire.

The effects of fire and canopy alteration extended beyond influencing just flower stalk production to also significantly increase fruit set and seed yield. Treatment with fire alone resulted in an approximate 50 – 100% increase in fruit set over control plants depending on inflorescence size, while combining canopy opening with fire yielded a general doubling in fruit production compared to controls. Effects on seed production were even greater, yielding two- to three-fold increases over the controls. Moreover, excess-seeded fruit production occurred almost exclusively in plants subjected to the experimental treatments, being most common in the open/fire strips. It is unclear whether this "supernumerary" seed production/fruit was the result of some type of polyembryony occurring in certain gynoecia (Bradley and Crane 1965, Willson and Burley 1983, Lovett Doust and Lovett Doust 1988) or incomplete fixation of the seed number/fruit character from that of *X. tenax*, which has a maximum possible yield of twelve seeds/fruit (Utech 1978). Utech (1978) stated that this higher seed production number in *X. tenax* was the evolutionarily ancestral condition, and the relatively small sample size of flowers used in his comparative anatomical study of these two congeners may have prevented his detection of supernumerary-seeded fruits in either species. Overall, these results convincingly reject the Fire/Canopy Alteration Effect null

hypothesis, demonstrating that the reproductive performance of *X. asphodeloides* was significantly enhanced through disturbance by fire and its associated canopy opening.

An equally important revelation is that the differences in the values of these reproductive variables correspond with findings on the pollination biology of the species. Bourg (in prep.) showed in artificial pollination experiments that *X. asphodeloides* is a predominantly outcrossing species. Hand-pollinated outcrossed flowers yielded a mean of 4 seeds/fruit whereas selfed flowers set less than 1 seed/fruit on average. Vance et al. (2004) obtained similar results in their investigation of the pollination biology of the congeneric *X. tenax* in Oregon. They characterized its mating system as one of 'leaky self-incompatibility' (Richards 1997) based on pollen tube growth abortions and the presence of very low but nonzero seed set in self-pollinated flowers. For the Orchid Hill *X. asphodeloides* population, open canopy/fire-treated plants produced 4.0 – 4.4 seeds/fruit depending upon inflorescence size, while shaded/fire-treated and control individuals set 3.3 and 2.5 seeds/fruit respectively, regardless of inflorescence size. The low seed yield/fruit numbers in the controls were consistent with the values from nearby undisturbed populations, in which the BMK2 individuals produced 1.7 seeds/fruit and the LRB plants yielded 2.6 seeds/fruit. The slightly higher yield in the LRB population could be attributable to the single year of data collection as well as the more open canopy at the LRB site, which lies at low elevation just inside the national forest boundary and is occupied by more recently regenerated forest (pers. obs.). Additionally, the very low seed yields (0.02 – 0.6 seeds/fruit) at Orchid Hill in the sparse flowering year of 2000, which occurred mostly in plants that had no possibility of experiencing a recent cost of

reproduction, are consistent with a dearth of outcrossing activity. It is difficult to argue

for the alternative explanation of resource limitation given the fact that all but one of

these individuals had the opportunity to uptake nutrients released by the fire before

flowering.


This increase in seed yield numbers in experimental treatment plants to levels

approaching or exceeding those obtained in the artificial outcross pollinations thus lends

support for the assertion that fire and its associated canopy opening encourage

outcrossing via insect vectors in *X. asphodeloides*, thereby providing a release from

pollinator limitation of reproduction (Bierzychudek 1981). The importance of such

environmental perturbations in influencing pollinator limitation has been recently

emphasized (Ashman et al. 2004). A possible mechanism for this release at Orchid Hill

could have been the presence of co-flowering plant species (Knight et al. 2005). Nectar-

rewarding plants, such as blueberries, flowered in abundance in the first several post-burn

years at the study site, and may have increased the insect pollinator community and

facilitated visitation to the nectarless turkeybeard flowers (Rathcke 1983, Laverty 1992,

Johnson et al. 2003, Moeller 2004, 2005). This was certainly the situation in the case of

the deceptive pink-lady's slipper orchid population at the site (Gill unpublished data).

Evans et al. (2003) showed such a pollinator limitation phenomenon for *Liatris*

*ohlingerae*, a fire-adapted Florida scrub herb that shares some life history traits with *X.*

*asphodeloides*. It should be noted however that Ne'eman et al. (2000) found significantly

lower pollinator visitation and fruit set in burned areas for three of four species of

Mediterranean scrubland herbs, although the study was conducted 5-7 years post-fire in

this habitat. Nonetheless, although the positive relationship between population density and reproduction known as the Allee effect (Allee et al. 1949) has customarily been described in social animals, evidence has been accruing for this phenomenon with regard to pollination in small or low flowering density populations in a number of plant species (Schaal 1978, Jennersten 1988, Kunin 1993, Lamont et al. 1993, Aizen and Feinsinger 1994, Bond 1994, Agren 1996, Groom 1998, Oostermeijer et al. 1998, Kearns et al. 1998, Spira 2001, Knight 2003). For *X. asphodeloides* in mature canopy forest, flowering, fruiting and seed production are significantly reduced and those fruits and seeds that do form are more likely derived from self-mating events in the absence of recent disturbance by fire.

*The Floral Density Effect Hypothesis:*

The results addressing the floral density effect hypothesis were more equivocal. The null contention of no difference in reproduction between relatively clumped and isolated plants could not be rejected in the Orchid Hill experimental individuals (**Tables 2 and 3**). Significant differences were found in seed production however among plants in undisturbed habitat, but the pattern was population dependent (**Figure 13**). Undisturbed plants in both the Orchid Hill and Long Run Bottom populations that were relatively isolated set more seed than those that were clumped, while the opposite was true for plants in the Benchmark2 population. Given the fact that turkeybeard is an insect-pollinated species that performs best when outcrossed (Bourg and Gill in prep.), the seed production and isolation effect findings together imply that undisturbed

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populations experienced pollinator limitation to seed set.  Disturbance by fire and canopy

alteration eliminated this constraint, because treated plants produced elevated and similar

seed yields regardless of their relative isolation from other flowering plants.


*The Floral Display Effect Hypothesis:*


The results of the analyses of the effect of flower stalk production on reproductive

performance supported a clear rejection of the floral display effect null hypothesis only

when plants produced at least five flower stalks.  There was a trend for plants with

multiple flower stalks, specifically 2-stalked plants, to produce both more fruits and more

seeds across all inflorescence sizes; however, such plants did not differ significantly from

single-stalked individuals.  Four-stalked plants produced significantly fewer fruits and

seeds than those with two stalks, although they did not differ significantly from 3-stalked

and 1-stalked plants.  However, plants with at least five flowering stalks deviated

significantly from the covariate by reproductive variable relationships displayed by the

other flower stalk categories.  The slope of this relationship was significantly less steep

for these plants, and in fact was nearly flat for seed production over the spectrum of

inflorescence sizes (**Figure 15**).  This may indicate a resource limitation threshold

(Abrahamson and Gadgil 1973) for flower stalk production, in which many (five or more)

stalks may benefit a plant by increasing its floral display size, but each additional stalk

reduces its capacity for supporting more seeds/inflorescence.  This was not the case,

however, for *X. asphodeloides* because there was little difference in mean seed

production per stalk across the flower stalk categories (**Figure 17**).  Additionally, plants

producing more than one stalk were still able to have significantly higher total seed yield than single-stalked individuals, and those with $\geq$ 5 stalks had the highest total per individual seed production (**Figure 16**).  Overall therefore, for *X. asphodeloides* it was advantageous to invest in floral display by producing multiple flower stalks because total seed yield was maximized, whether on a per flower stalk basis, as in doublets, or on a total plant basis.  Such exceptional flowering typically occurred in fire- and canopy alteration-treated plants, where the flower stalk production per plant was frequently 2 or more, while flowering plants in undisturbed habitat usually only grew a single flower stalk.
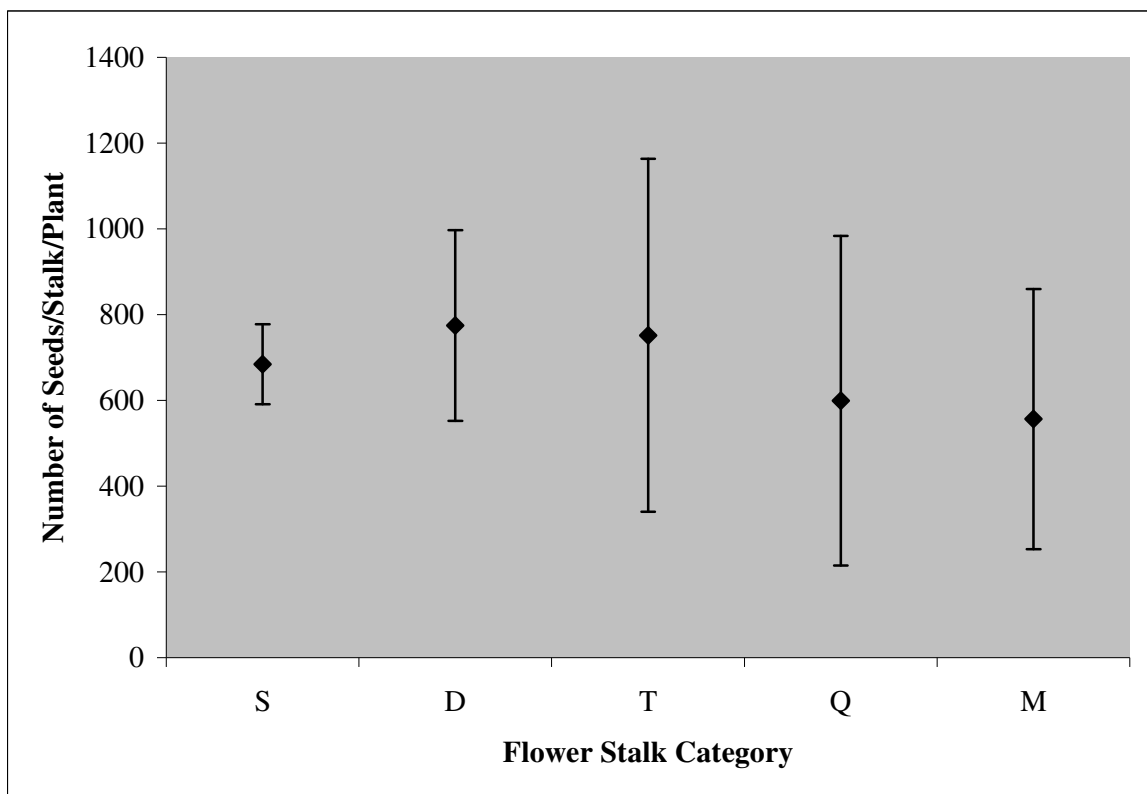


**Figure 17.**  Mean seed production per stalk per plant for the five flowering stalk categories used in the analyses of the effect of multiple flower stalks on reproductive performance at Orchid Hill in the 1998 and 1999 response years.  Bars indicate 95% confidence intervals.  S = single-stalked plants, D = double-stalked plants, T = triple-stalked plants, Q = quadruple-stalked plants, and M = $\geq$5-stalked plants.

Finally, the results of the estimation of fire history from multiple turkeybeard localities confirmed an association with repeated disturbance by fire on at least an ecological time scale (**Table 8**).  Although an evolutionarily relevant relationship is much more difficult to obtain, the fire effects documented in this study as well as the species' morphological attributes and frequent habitat co-occurrence with fire-adapted pines and oaks all lend strong support for characterizing *X. asphodeloides* as one of the few fire-adapted forest herbs in the eastern United States.  Because fire's role as a disturbance agent in these eastern forests has generally been under appreciated, particularly in the central and southern Appalachians, until very recently, these findings are important not only for the autecology and conservation of this unique plant but also for their potential contribution to furthering our understanding of disturbance regimes and their management implications for this large and diverse forest ecosystem.

The implications of this study for ecologically based management of the southern Appalachian forest ecosystem are substantial.  Even though Virginia comprises the stronghold for the species in these mountains, the number and extent of *X. asphodeloides* population occurrences either here or in the rest of its Appalachian range are only partially known.  For example, turkeybeard is found on both the George Washington National Forest and Shenandoah National Park, yet the precise locations, sizes and frequency of the occurrences have not been determined (S. Croy pers. comm., D. Raeburn pers. comm., D. Hurlbert pers. comm.).  A number of populations exist on the Jefferson National Forest (JNF) to the south (S. Croy pers. comm.), and there are probably multiple populations present on the Glenwood/Pedlar Ranger District of the

GWNF/JNF, which lies immediately to the south of SNP on the Blue Ridge and has the highest frequency of historic lightning-caused fires of any GWNF district (USFS 1997). The species is also somewhat common on national forest lands in western North Carolina (WVNHP 1995a, b; CPC 2004). This study has shown that populations of this species are discrete, often large in both numerical as well as spatial terms, and highly likely to be indicative of a fire-dominated historical disturbance regime.

Turkeybeard's western congener beargrass (*X. tenax*), has long been used as an indicator species of various forest types in vegetation classification schemes for the western U.S. (Pfister et al. 1977, Steele et al. 1981, 1983; Cooper et al. 1987, Bourgeron and Engelking 1994, Williams et al. 1995, Kagan et al. 2004). It currently is a defining species for 34 vegetation types at the association level under the National Vegetation Classification Standard (FGDC 1997, Grossman et al. 1998, NatureServe 2005). However, turkeybeard has not been used in this way thus far in natural community classification in Virginia (Fleming et al. 2005). The results of this study suggest that consideration should be given to similar use of *X. asphodeloides* as an indicator species in Appalachian forests. Toward this end, Bourg et al. (2005) recently developed a predictive habitat model for *X. asphodeloides* on the three northernmost districts of the GWNF. In addition to classifying nearly 9,000 ha of this study area as suitable habitat for turkeybeard, the modeling effort yielded the discovery of eight new populations during ground-truthing exercises. Refinement and application of such modeling techniques to other areas of the Appalachians could contribute greatly toward employing *X. asphodeloides* as an indicator species of fire-influenced habitat types and lead to

improved planning for ecosystem management and better targeting of prescribed fire

programs.

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**Chapter 2**


**Pollination Biology of Turkeybeard (*Xerophyllum asphodeloides*) (L.) Nutt. (Melanthiaceae) in the Context of Fire in the Appalachian Mountains of Virginia, U.S.A.**

**Pollination Biology of Turkeybeard (*Xerophyllum asphodeloides*) (L.) Nutt. (Melanthiaceae) in the Context of Fire in the Appalachian Mountains of Virginia, U.S.A.**

**Abstract:**

*Xerophyllum asphodeloides* is a rare, fire-adapted forest herb found primarily in the southern Appalachians and disjunctly in the New Jersey Pine Barrens. This species reproduces infrequently in undisturbed forest, but mass flowers following disturbance by fire and its associated canopy opening. The pollination biology of *X. asphodeloides* within the context of fire was studied through controlled hand pollination experiments and incidental pollinator observations and collections over three flowering seasons. Cerambycid beetles were the most diverse group of pollinators collected from inflorescences, followed by bees, which were also observed undertaking longer distance cross-pollinations between genets. Hand-pollinated outcross treatments produced consistently high levels of seed set/fruit, while open-pollinated natural controls exhibited considerably more inter-annual variability. Seed set in open-pollinated flowers was high and similar to hand-outcrossed flowers in fire-induced mass flowering years, but was low and similar to self-pollination treatments in years of sparse flowering. In concordance with a recent study of the congeneric beargrass (*X. tenax*), the mating system of *X. asphodeloides* appears to be that of a primarily outcrossing species with "leaky" self-incompatibility, because of low but non-zero seed production occurring in self-pollinated flowers. Populations typically exhibit low flowering levels in undisturbed forest which in combination with their self-incompatibility subjects them to Allee effects due to

pollinator limitation in most years.  Disturbance by fire results in release from these limiting factors by altering the forest habitat to attract insect pollinators that then visit the mass-flowering plants, thus facilitating outcrossing and seed set in this rare species.  In addition to providing valuable information on the breeding system of the only remaining unexamined species of *Xerophyllum*, the results of this study are important for conservation and management efforts because they have shown the importance of the interaction of disturbance by fire with insect-mediated outcrossing for successful seed production in *X. asphodeloides*.

**Introduction:**

The phenomenon of pollen limitation has often been invoked as a major factor that could influence plant reproductive performance in nature (Bierzychudek 1981, Burd 1994, Larson and Barrett 2000, Ashman et al. 2004, Knight et al. 2005).  The presence of this phenomenon would be expected to be particularly important for populations of plant species in decline or listed as endangered, threatened or of conservation concern.  In addition, recent reviews have emphasized the role that environmental perturbations might play in pollen limitation (Ashman et al. 2004, Knight et al. 2005).

In two separate recent studies, Bourg et al. (2005) and Bourg et al. (unpub. ms) have shown that fire plays a crucial role in the biology of the rare Appalachian forest herb turkeybeard (*Xerophyllum asphodeloides*) at both the landscape and population levels,

through its association with suitable habitat and its effects on flowering, fruit and seed set. Nothing was known about the pollination biology or mating system of this species when these studies were being conducted, however. The impetus for the present study was to provide information on the breeding system of *X. asphodeloides* in the context of a fire and canopy alteration experiment that was undertaken to examine the fire ecology of this species by Bourg et al. (unpub. ms). Forming a more complete understanding of the factors that determine and/or limit the reproductive performance of turkeybeard would be important for its conservation and management, since it is endangered or rare in a number of states in the Appalachian portion of its range and is included in the National Collection of Endangered Plants (CPC 2004, NatureServe 2005).

Vance et al. (2004) recently published the first in-depth study of pollination biology in the genus *Xerophyllum* for beargrass (*X. tenax*) (Pursh.) Nutt., a common and charismatic forest herb of the northern U.S. and southern Canadian Rocky Mountains, the Pacific Northwest, and northern California (Hitchcock and Cronquist 1973, Utech 1978). This congener is allopatric but morphologically similar to *X. asphodeloides*, which is more rare and found in the Appalachian Mountains from Virginia to northern Alabama as well as disjunctly in the New Jersey Pine Barrens (Utech 1978, WVNHP 1994, 1995a, b; NatureServe 2005). There were two main motivations for Vance et al.'s study of *X. tenax*. The first was to contribute to better management and conservation of this species, because although beargrass is a characteristic understory component of many western U.S. forest types, populations could be detrimentally impacted by forest management practices and commercial harvesting of leaves for the floral industry and indigenous

basketry trade (Dimock 1981, Hunter 1988, Johnson 1992, Moerman 1998, Turner 1998, Mosley 2000, Vance et al. 2001). The second objective involved determining the breeding system to contribute to a better understanding of the phylogenetic placement of *Xerophyllum* within the Liliales. In the most recent phylogenetic revision of this order, Rudall et al. (2000) placed *Xerophyllum* into the Melanthiaceae based on a combined morphological and molecular character analysis. However, its position within the family had only moderate support and, somewhat surprisingly, it was determined to be a sister genus to *Paris* and *Trillium*, genera typified by a large, solitary, and usually sessile mode of floral presentation. Of particular relevance is the recent finding by Sage et al. (2001) of an early acting, 'leaky' stigmatic self-incompatibility system in *T. grandiflorum* and *T. erectum*. Including the study of Vance et al. (2004), such gametophytic self-incompatibility has now been definitively established in only five monocot families (Commelinaceae, Liliaceae, Melanthiaceae, Bromeliaceae, and Poaceae), using the Rudall et al. (2000) classification of the Trilliaceae into the Melanthiaceae is used (Sage et al. 2000). Further knowledge of the breeding systems of *Xerophyllum* would therefore also be useful for refining the phylogeny of the Liliales.

**Methods:**

*Study species:*

Turkeybeard (*X. asphodeloides*) is an acaulescent, geophytic, perennial monocot that grows predominantly in pine (*Pinus* spp.) and mixed pine-oak (*Quercus* spp.) forests of the southern central and southern Appalachian Mountains as well as in the Pine Barrens of New Jersey (Harshberger 1916, CPC 2004, NatureServe 2005). Bourg et al. (2005) developed a predictive habitat model for the species in the mountains of northwestern Virginia, which indicated that populations were characterized primarily by the four main explanatory variables of elevation, slope, forest type, and fire frequency. Populations occurred either at high elevation on low to moderate slopes or in a mid-elevation range on similar slopes in mainly pine and xeric pine-oak forest types with higher fire likelihood. The plant itself is comprised of a short, stout rhizome terminated by one or more closely connected tunicate bulbs that arise from meristems on its dorsal surface (Ambrose 1975). The long, grass-like, evergreen leaves arise spirally from these meristems, numbering in the hundreds if not thousands in large specimens. Individuals can remain in an aboveground, vegetative or infrequently flowering state for multiple seasons in undisturbed closed canopy forest, but mass flowering is induced in the second and third years following a fire (Bourg et al. unpub. ms).

*X. asphodeloides* is in general a less robust plant than its western congener *X. tenax* (Utech 1978). While *X. asphodeloides* and *X. tenax* are highly similar in gross morphology, they do differ in finer details of their floral presentation and structure. Both species have inflorescences consisting of a terminal conical raceme of many small, perfect, white flowers. The *X. asphodeloides* inflorescence, however, typically has only half as many flowers (approximately 200 on average) that are more restricted toward the distal end of the elongate flowering stalk. The flowering stalk of *X. asphodeloides* can extend up to 1.5m in height above the base of the leafy base of the plant. Flowering is centrifugal with the lowest, proximal flowers undergoing anthesis first and distal flowers opening last. Each flower of a turkeybeard inflorescence attaches to the flowering stalk by means of a pedicel that averages 3 cm in length and consists of six oblong tepals that lack nectary glands. As in *X. tenax*, the gynoecium is tricarpellate with three free, recurved styles but each carpel characteristically contains only two seeds per locule in turkeybeard, whereas beargrass has four seeds/locule (Utech 1978).

*Study site:*

Experiments and collections were done at Orchid Hill, a long-term study site with a marked *X. asphodeloides* population located at 763m a.s.l on the Dry River Ranger District of the George Washington National Forest (GWNF), Rockingham County, Virginia (Gill 1989, 1996; Bourg et al. 2005). The forest here is mixed conifer-hardwood forest dominated by table mountain pine, chestnut oak (*Quercus montana = prinus*), and pitch pine (*P. rigida*) with an understory shrub layer composed mainly of bear oak (*Q.*

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*ilicifolia*), early low-bush blueberry (*Vaccinium vacillans*), black huckleberry (*Gaylussacia baccata*), mountain laurel (*Kalmia latifolia*), and mountain fetterbush (*Pieris floribunda*). *X. asphodeloides* flowers here from mid-May until early July.

*Foraging insects:*

Incidental observations and collections of potential insect pollinators visiting turkeybeard inflorescences in the population were made over the course of the study. Insects were captured from inflorescences as they were encountered by hand or with forceps, placed in capped glass vials, and killed with fumes of ethyl acetate. Pinned specimens were taken for identification to the following laboratories: Coleoptera (S.W. Lingafelter, Systematic Entomology Laboratory, USDA-ARS/PSI, National Museum of Natural History, Washington, DC, USA); Coleoptera, Diptera, and Hemiptera (RW. Carlson and E.C. Kane, Communications and Taxonomic Services Unit, Systematic Entomology Laboratory, Beltsville Agricultural Research Center (BARC), USDA-ARS, Beltsville, MD, USA), and Hymenoptera (S. Droege, U.S. Geological Survey, Patuxent Wildlife Research Center, BARC-East, Beltsville, MD, USA).

*Hand pollination experiments – design and techniques:*

Controlled pollination experiments were conducted at this site during the 1997, 1998 and 1999 flowering seasons. In 1997 and 1998, the experiments were designed as randomized complete blocks with replication, with the inflorescence serving as a block

and the following treatments installed on each inflorescence: 1) Selfing – both autogamous selfing (AS; pollen from a flower's dehisced anthers was applied to its own stigma) and geitonogamous selfing (GS; pollen from dehisced anthers of others flowers on the same inflorescence was applied to the stigmas of emasculated flowers) were applied in 1997. A single selfing treatment (SELF) consisting of a mixture of autogamous and geitonogamous pollen was used in 1998. 2) Within-population hand cross pollination (WX) – in both 1997 and 1998, flowers were emasculated, and pollen from dehisced anthers of flowers on other inflorescences in the Orchid Hill population was applied to the stigmas of these emasculated flowers; 3) Between-population hand cross pollination (BX) – in 1998 only, flowers were emasculated and pollen from dehisced anthers of flowers on inflorescences in a population 3.5km distant was applied to the stigmas of emasculated flowers; 4) Emasculation Sham Control (SC) – in both 1997 and 1998, flowers were handled in a similar manner as in the above treatments and emasculated but no pollen was applied to their stigmas; and 5) Natural Control (NC) – in both 1997 and 1998, unmanipulated and unemasculated flowers were exposed to pollinators. A total of seven inflorescences served as blocks in 1997 and five inflorescences were used as blocks in 1998. Due to the low overall flowering levels in the population in 1997, three of the plants in this year were located in the undisturbed, control portion of the study site, while the remaining four plants were in one of the canopy removed, burnt portions. All plants used in the 1998 experiment were located in canopy removed, burnt portions of the area. Plants with a single flowering stalk were used in each of these years and vegetative size and flower stalk height measurements

were recorded for potential use as covariates.  Each experimental treatment was replicated three times per inflorescence, while the NC was replicated nine times.

During the 1999 flowering season, another controlled pollination experiment was conducted to examine whether any evidence could be obtained for a density-dependent effect of outcrossing on seed set in hand pollinated flowers.  This experiment was installed as a nested randomized design with plants nested within treatment and each inflorescence receiving only one of the following four treatments:  1)  Selfing (9S) – nine flowers were selfed on an inflorescence with a mixture of autogamous and geitonogamous pollen; 2)  Low density hand cross pollination (3X) – three flowers on an inflorescence were emasculated and then outcrossed with pollen from inflorescences found in the same 3.5 km distant population used in 1998; 3)  Medium density hand cross pollination (9X) – nine flowers on an inflorescence were emasculated and then outcrossed with pollen from inflorescences found in the same long distance population; and 4)  High density hand cross pollination (27X) - twenty-seven flowers on an inflorescence were emasculated and then outcrossed with pollen from inflorescences found in the same long distance population.  In addition, nine unmanipulated and unemasculated flowers to which pollinators had been allowed open access were collected from each inflorescence used in the above treatments to serve as natural controls (NC). An emasculation sham control (SC) treatment was omitted in this year to make available more inflorescences for outcross treatments, after analysis of the 1997 and 1998 experiments showed that SC treatments had virtually identical performance as selfed treatments in both years.  This might be expected in bagged inflorescences of a species

such as *X. asphodeloides*, where flowers are tightly packed on a conical inflorescence and undergo anthesis sequentially from bottom to top. Twenty-one single-stalked plants all located in shaded, burnt habitat on the north slope of the study site were used in this experiment. These plants were chosen because they were all in nearly identical stages of inflorescence maturation (i.e., in bud) at the initiation of the experiment. Vegetative size and flower stalk height measurements were again recorded for potential use as covariates.

In all three years, experimental inflorescences were first inspected to remove any insects present and then isolated in plastic mesh bags (Applied Extrusion Technologies, Wilmington, DE) fastened to the inflorescence stalk with twist ties to prevent any further insect visitation. In 1998 and 1999, lengths of ¼" wooden dowels were inserted into the ground next to each plant and clear plastic 16 oz. wide-mouth cups were suspended from their top end above the apex of the inflorescence to aid in preventing a bag from contacting its inflorescence. Bags were temporarily removed from each inflorescence at the time of treatment application. For the GS treatment as well as the allogamous pollen supplementation treatments and SC treatments, recently opened flowers with preferably undehisced anthers were identified and emasculated by grasping the filament of each stamen at approximately mid-length with a pair of fine-tipped forceps and pinching it off. For the AS treatment, one to several stamens with freshly dehiscent anthers were excised in similar fashion from their respective flowers and used to pollinate their stigmas. For flowers in the GS treatment, stamens with dehiscent anthers from other flowers on the same inflorescence were utilized in a similar manner for pollination of their stigmas. In the single SELF treatment of 1998, a combination of the previous two techniques was

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used for pollination.  Stamens with dehiscent anthers were removed in the same fashion

from other plants of either the same or different population, collected in capped glass

vials, and used to pollinate the stigmas of flowers in the WX and BX, 3X, 9X, and 27 X

treatments respectively.    Prior to application, stigmas of all flowers were visually

examined, with a 10x Coddington hand lens where necessary, to ensure that they were

clean of pollen.


In 1997 and 1998, a short length of uniquely colored sewing thread was tied

loosely to each flower's pedicel after a given treatment was applied.  A minute dot of

orange acrylic model paint was placed on the main inflorescence stalk immediately below

the emergence point of a given treated flower's pedicel to mark experimental flowers in

1999.  Mesh bags were replacedonto each inflorescence after treatment installation was

completed and then removed either when fruits were mature (1997 and 1998) or after

stigmas were withered, dried and no longer receptive (1999).  Flowers that had been

exposed to pollinators prior to bagging were identified and marked as natural controls

(NC) in 1997 and 1998, and in these years all treatments were installed on the same day,

either in the first week of June (1997) or last week of May (1998).  In 1999, treatments

were installed on seven different days over a twelve-day period in early June, depending

upon the rate of anthesis of each inflorescence. Natural controls were identified and

marked after bag removal in 1999.

*Statistical analyses:*

The seed count data were analyzed using SAS Version 9.0 statistical software (SAS Institute Inc. 2002).  Examination of the relationships between number of seeds/fruit in 1997 and 1998 and the potential covariates of vegetative size and flower stalk height showed no significant covariate effect, so tests for treatment differences were conducted as randomized complete block designs (RCBD) with replication, mixed model analyses of variance (ANOVAs).  Replication of treatments within blocks enabled both the block and block*treatment interaction to be extracted as random sources of variation. In 1999, the test for treatment differences in the pollination experiment was done as a nested mixed model analysis of covariance (ANCOVA) with samples nested within plant and then plant nested within treatment.  Because the experiment was set up over multiple days, the treatment installation date was used as a covariate in this analysis.  Natural log transformation of data was performed where necessary to meet ANOVA assumptions of homogeneity of variances and normality.  If transformation was still unsuccessful in bringing data into conformity with these assumptions, a non-parametric Friedman's rank 2-way ANOVA was utilized instead to test for treatment differences (Sokal and Rohlf 1995).

**Results:**

*Foraging insects:*

Incidental collections of prospective pollinators found on turkeybeard inflorescences resulted in 86 individuals from five insect orders being amassed (**Table 1**). Beetles (Coleoptera) were the most abundant and diverse group. A species of cerambycid flower beetle (*Euderces* sp.) was the most numerous single taxon, followed closely by a species of mordellid beetle. Overall, cerambycid beetles were the most diverse family of visitors. Thrips (Thysanoptera) were the next most commonly collected group. Pentatomid and membracid bugs (Hemiptera) were next in abundance. Four species of solitary bees (Hymenoptera) in the Andrenidae and Halictidae were collected and identified. Additional individuals of these species were often observed gathering pollen from turkeybeard flowers, particularly *Andrena milwaukiensis* and *A. barbara*. Lastly, true flies (Diptera) were the most infrequently represented insects that were collected, represented by one specimen each of a hover fly (Syrphidae) and a bee fly (Bombylliidae).

**Table 1.** List of insects collected from flowers of *X. asphodeloides* in the 1997, 1998, and 1999 flowering seasons at the Orchid Hill study site, GWNF, VA.

| Insect Taxon | Number of Individuals |
|---|---|
| Thysanoptera | |
|   Thrips sp. | 12 |
| | |
| Hemiptera | |
|   Pentatomidae | |
|     Sp. 1 | 4 |
|   Membracidae | |
|     Sp. 1 | 2 |
| | |
| Coleoptera | |
|   Cerambycidae | |
|     *Euderces picipes* (Fabricius) | 20 |
|     *Molorchus bimaculatus* Say | 6 |
|     *Encyclops caerulea* (Say) | 4 |
|     *Judolia cordifera* (Olivier) | 3 |
|     *Analeptura lineola* (Say) | 1 |
|     *Callimoxys sanguinicollis* (Olivier) | 1 |
|     *Cyrtophorus verrucosus* (Olivier) | 1 |
|     *Strangalepta abbreviata* (Germar) | 1 |
|   Scarabaeidae | |
|     *Trichiotinus* sp. | 1 |
|   Mordellidae | |
|     Sp. 1 | 19 |
|     Sp. 2 | 3 |
|   Chrysomelidae | |
|     Sp. 1 | 1 |
|   Elateridae | |
|     Sp. 1 | 2 |
|     Sp. 2 | 1 |
|   Oedemeridae | |
|     Sp. 1 | 1 |
|   Cantharidae | |
|     Sp. 1 | 2 |
| | |
| Diptera | |
|   Bombylliidae | |
|     Sp. 1 | 1 |
|   Syrphidae | |
|     Sp. 1 | 1 |
| | |
| Hymenoptera | |
|   Andrenidae | |
|     *Andrena milwaukiensis* | 2 |
|     *A. barbara* | 1 |
|   Halictidae | |
|     *Lasioglossum acuminatum* | 1 |
|     *L. rohweri* | 1 |

*Pollination experiments:*

Hand outcross pollinations produced consistently high levels of seed set/fruit in all three study years irrespective of whether within-population (short distance outcross) or between-population (long distance outcross) pollen was used, whereas seed yield in natural control (NC), open-pollinated flowers showed substantial inter-annual variation with only 1998 having high seed set (**Figure 1**). In the 1997 experiment there was a significant treatment effect ($F_{(4, 24.6)} = 4.65$, $p = 0.006$), with the within-population outcross treatment (WX) producing significantly more seeds/fruit than any of the other treatments. There was no significant difference among autogamously selfed (AS), geitonogamously selfed (GS), sham control (SC), and natural control (NC) flowers (**Figure 2**). These data had heterogeneous variances even when ln transformed however, so a non-parametric Friedman's rank 2-way ANOVA was also conducted and once again produced a significant treatment effect due to the high yield in the WX treatment ($F_{(4, 24)} = 7.99$, $p < 0.0001$).
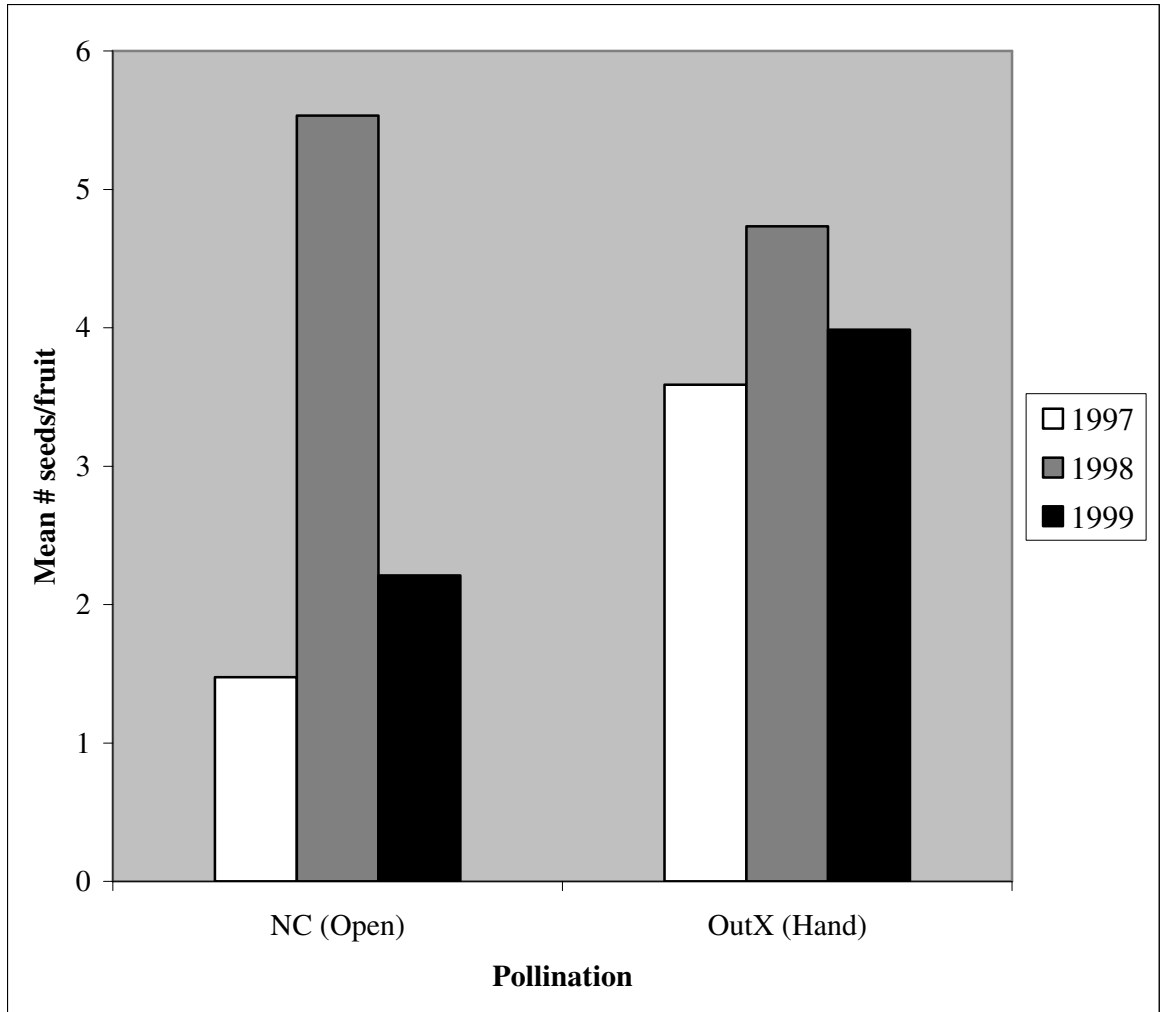
**Figure 1.** Comparison of mean seed production/fruit in natural control, open-pollinated flowers (NC) with hand outcrossed flowers (OutX) from the pollination experiments conducted on *X. asphodeloides* inflorescences at Orchid Hill, George Washington National Forest (GWNF), Rockingham Co., VA in 1997, 1998 and 1999.
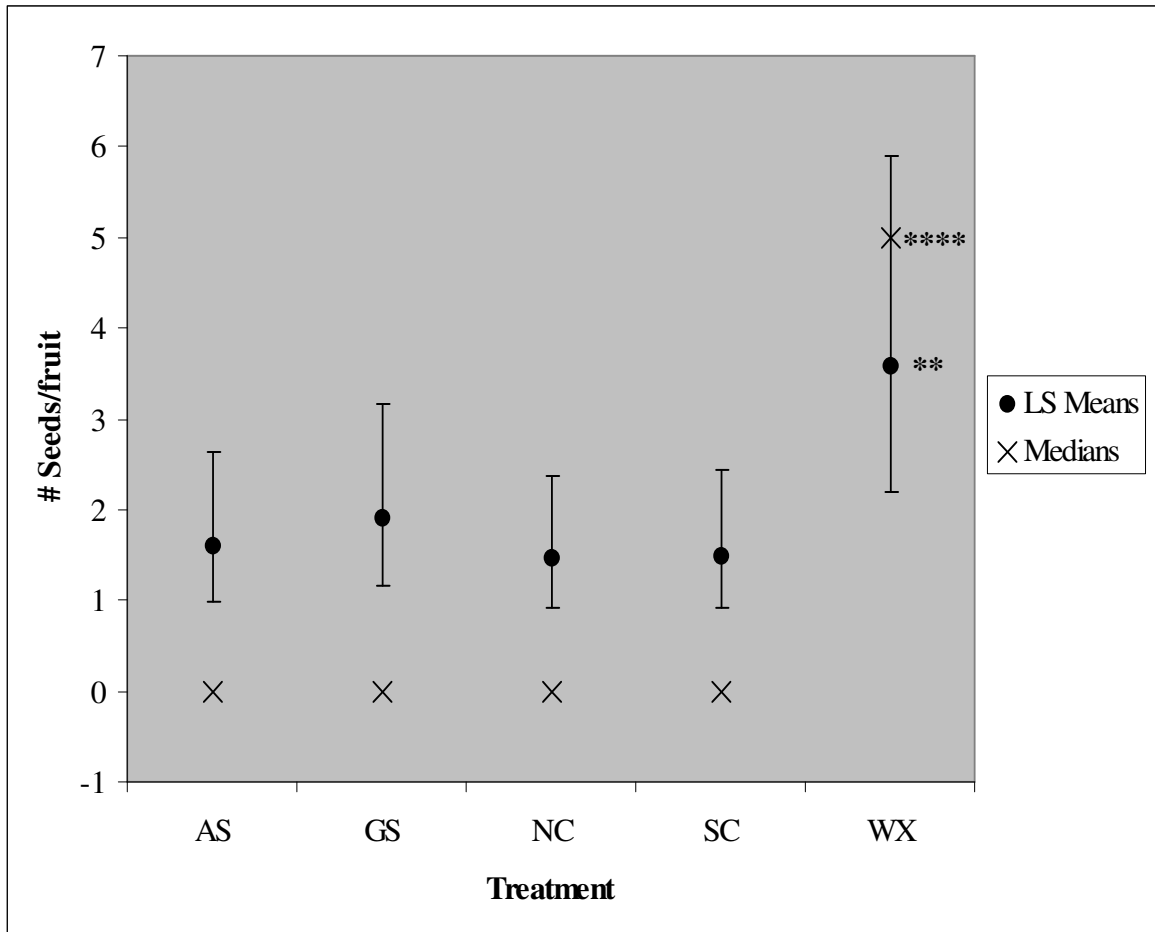
**Figure 2.** Number of seeds/fruit produced in the five treatment categories from the 1997 hand pollination experiment (AS = autogamous self, GS = geitonogamous self, NC = natural control or open-pollinated, SC = emasculation sham control, and WX = within-population outcross). Two value series are shown - LS Means are the back-transformed least-square means from the ANOVA analysis of ln-transformed values; Medians are the median values from the non-parametric Friedman's 2-way ANOVA analysis. Bars indicate 95% confidence intervals. ** = p<0.01, **** = p<0.0001.

Treatments in the 1998 pollination experiment performed differently from the 1997 results (**Figure 3**). There was again a significant treatment main effect in 1998 ($F_{(4, 15.1)}$ = 3.61, p = 0.03), with SELF and SC treatments having similar low seed yield/fruit while both outcross treatments (WX and BX) and the natural controls (NC) had similar high seed yields/fruit. Between these low and high seed yield groupings, pairwise mean comparison tests showed that the NC category produced significantly more seeds/fruit

than both the SC and SELF treatments ($F_{(1, 13.2)}$ = 9.67, p = 0.008 and $F_{(1, 13.2)}$ = 8.34, p = 0.01 respectively), the WX treatment had significantly greater production than the SC treatment only ($F_{(1, 17.5)}$ = 4.57, p = 0.047), and the BX treatment did not differ significantly from either the SC or SELF treatments.
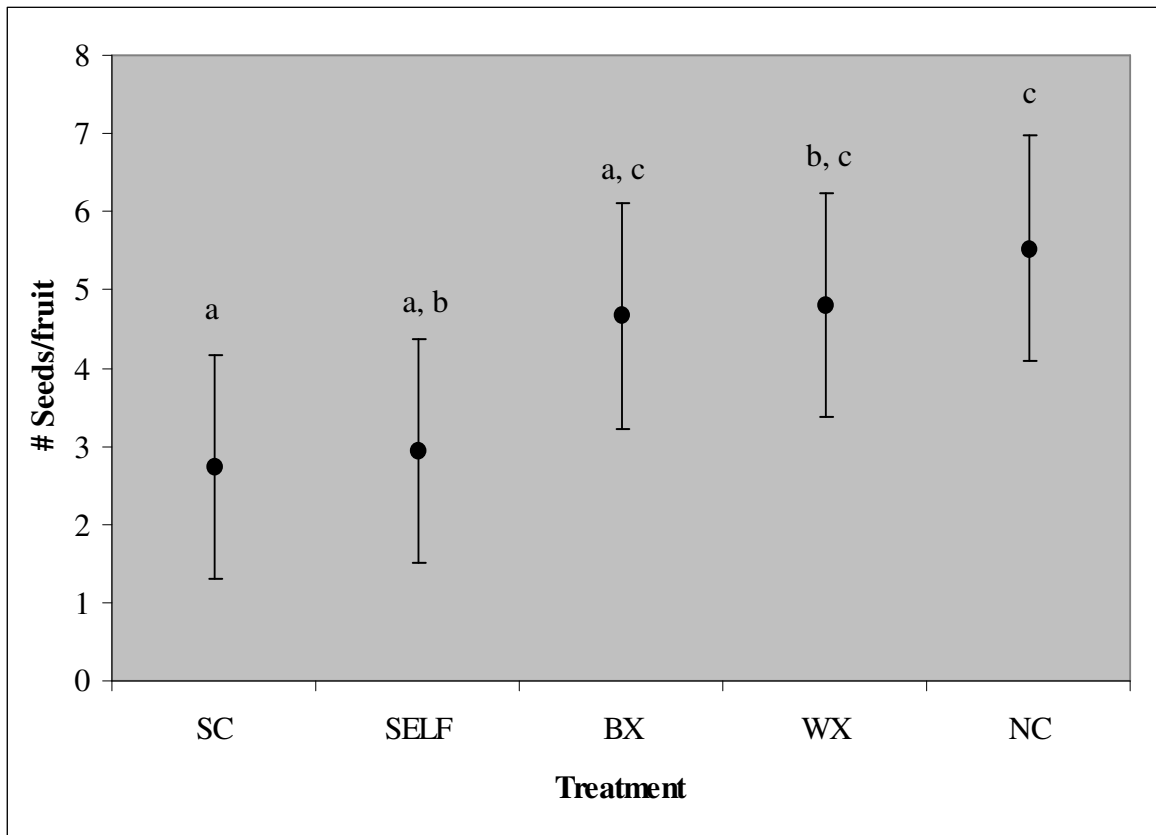


**Figure 3.** Number of seeds/fruit produced in the five treatment categories from the 1998 hand pollination experiment (SC = emasculation sham control, SELF = mixture of autogamous and geitonogamous self, BX = between-population outcross, WX = within-population outcross, and NC = natural control or open-pollinated). Treatments sharing letters are not significantly different at $\alpha$ = 0.05.

Treatments performed somewhat differently in relation to each other once again in the pollination experiment of 1999 (**Figure 4**). First, there was a significant effect of the covariate of treatment installation date on seed yield/fruit ($F_{(1, 333)}$ = 5.84, p = 0.016). Second, although as in previous years there was a significant treatment main effect ($F_{(4,}$

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$_{36)}$ = 7.44, p = 0.0002), pairwise mean comparison tests showed that all outcross

treatments as well as the natural controls (NC) produced significantly more seeds/fruit

than the 9S selfed treatment ($F_{(1, 36)}$ = 14.14, p = 0.0006; $F_{(1, 36)}$ = 18.34, p = 0.0001; $F_{(1,}$

$_{36)}$ = 11.93, p = 0.0014; and $F_{(1, 36)}$ = 5.34, p = 0.0267 for 3X, 9X, 27X and NC treatments

respectively).  Furthermore, all of the outcross treatments performed significantly better

than the NC group ($F_{(1, 36)}$ = 7.11,  p = 0.0114; $F_{(1, 36)}$ = 11.70, p = 0.0016; $F_{(1, 36)}$ = 5.04, p

= 0.0310 for 3X, 9X and 27X treatments respectively), but did not differ amongst

themselves.
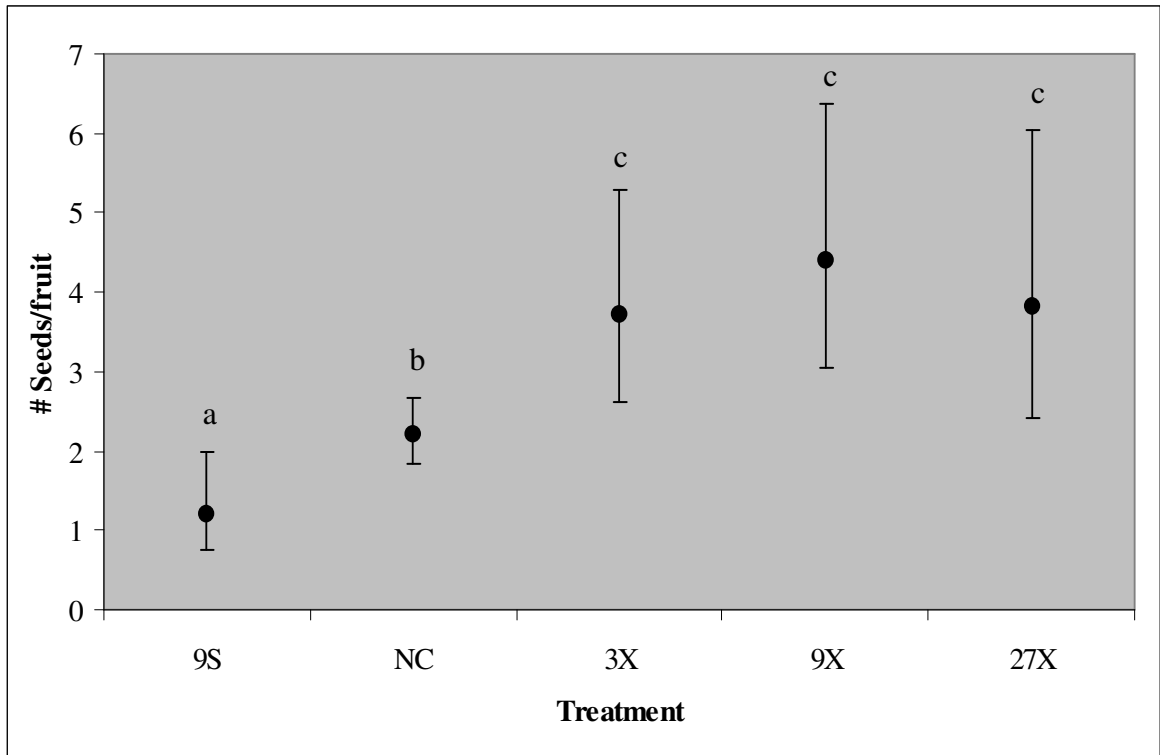
**Figure 4.** Number of seeds/fruit produced in the five treatment categories from the 1999 hand pollination experiment (9S = self, NC = natural control or open-pollinated, 3X = between-population outcross 1, 9X = between-population outcross 2, and 27X = between-population outcross 3). Treatments sharing letters are not significantly different at $\alpha = 0.05$; b differs from a and c at the 0.05 level, a differs from c at at least the 0.01 level.

**Discussion:**

The variety of insects obtained from incidental collections on turkeybeard flowers was broadly similar to the results of Vance et al. (2004) for *X. tenax*, at least in terms of representation of the typical important major pollinator orders Coleoptera, Diptera and Hymenoptera (**Table 1**). The cerambycid beetle *Euderces* sp., the most commonly collected insect, was observed moving among flowers on a given inflorescence often as well as flying between inflorescences of separate plants less often. Mordellid beetles

were also commonly observed on and collected from turkeybeard flowers, but the extent of their movement between inflorescences could not be ascertained due to their small size. They frequently dropped passively to the ground when attempts were made to capture them, and they usually seemed to be residing near the base of flower corollas rather than moving among the stamens and stigmas. The main difference in our pollinator observations from the pollinator findings for beargrass (Vance et al. 2004) however was the under representation of syrphid dipterans in the present study. Syrphids are strong, agile fliers that spend little residence time on an inflorescence in a given visit and as such are more difficult to observe and capture incidentally, but they were noted on inflorescences at Orchid Hill more frequently than the collection data suggests (pers. obs.). More systematic surveys using nets to collect insect specimens might have revealed greater abundances of syrphids at Orchid Hill. Lastly, bees were also infrequently collected yet they were the most commonly noted transporters of pollen between inflorescences (pers. obs.). For instance, on two separate occasions in 1999 a total of five andrenid bees were observed collecting pollen on inflorescences, and four of these were watched as they flew their visibly pollen-laden bodies multiple meters onto from 1-3 other inflorescences of separate turkeybeard plants in succession. In addition, on another occasion a bumblebee (*Bombus* sp.) was seen collecting pollen on a turkeybeard inflorescence. In summary, the foraging insect pollinator results agree with the assertion by Vance et al. (2004) of a beetle-pollinated, "brush mode" of floral presentation (Bernhardt 2000) in *X. tenax*, with bees and flies playing an occasional but important role in longer-distance cross pollinations. Further survey work is needed to

elucidate whether dipteran visitation to turkeybeard flowers in the Appalachians is as common as it is on beargrass flowers in the Cascade Mountains of Oregon.

In general, the results of this multi-year study demonstrated that hand-supplemented outcross pollinations of *X. asphodeloides* flowers were successful and repeatable in achieving high levels of seed set over three flowering seasons (**Figure 1**), whereas seed set was repeatedly low in selfed treatments across the years (**Figures 2 –4**). Such results have traditionally been taken as strong evidence for self-incompatibility and thus the results for *X. asphodeloides* are interpretable in similar fashion.  They also conform well with one of the findings of Vance et al. (2004), who demonstrated that the congeneric *X. tenax* was self-incompatible based on significant differences in pollen tube growth rates in hand pollinated selfed vs. outcrossed flowers.  Pollen tube growth was not examined in *X. asphodeloides* in this study to confirm the site of the self-incompatibility. The fact that low seed yields were obtained from selfed treatments also concurs with the findings of Vance et al. (2004) for beargrass, who determined that it possessed an early-acting, "leaky" self-incompatibility system (Richards 1997) similar to that described by Sage et al. (2001) in *Trillium* spp.  The emasculation sham controls (SC) performed in the present study further suggested that this is also likely to be the case for *X. asphodeloides* because they produced seed in the same amounts as selfed treatments, even though the expectation was no seed set since their anthers had been removed prior to the onset of stigma receptivity.  This can be most readily explained by the potential for geitonogamous pollen transfer in bagged inflorescences, although the less likely possibility of a low but persistent rate of agamospermy cannot be excluded.  Evaluation

of pollen tube growth in hand-pollinated flowers as well as examination of ovule development should be conducted in the future to provide definitive confirmation of self-incompatibility.

Additionally, the consistently high cross-pollination seed yields/fruit in turkeybeard contrasted markedly with natural amounts of seed production/fruit from open-pollinated flowers during the same time period, which exhibited much greater variability (**Figure 1**). In the population and habitat contexts under which the experiments in the present study were undertaken, this finding points to pollination limitation as a significant factor in the biology of *X. asphodeloides*, and thereby exposed a new facet to the interpretation of the pollination biology of this genus begun by Vance et al. (2004). In terms of the population context, the 1997 experiment was conducted in one of the lowest flowering years recorded over the sixteen-year Orchid Hill long term population monitoring dataset, when only 10 turkeybeard plants out of a total marked population of 690 individuals reproduced with a single inflorescence each (Bourg et al. unpubl. ms). In the context of habitat, four of the 1997 experimental plants had been burnt immediately prior to the 1996 season while the remaining three were in undisturbed forest. In contrast, the 1998 and 1999 experiments occurred during the two largest flowering years on record, when 140 and 236 individuals flowered respectively, many of which produced multiple inflorescences. Also, all of the plants used in the pollination experiments in these two years had been subject to the 1996 burn.

The environment for insect pollinators at Orchid Hill was of low quality in 1997 because the ericaceaous understory was in a predominantly vegetative stage of regrowth from the 1996 fire (pers. obs.). Hence in the 1997 experiment the open-pollinated NC flowers were embedded in a depauperate pollinator environment, and in turn the insect community was presented with a paltry population-level turkeybeard floral display. Taken together, this explains the low seed set found in NC fruits that did not differ from selfed treatments (**Figure 2**). By the 1998 and 1999 flowering seasons the understory vegetation, particularly the blueberries and huckleberries, flowered in great quantity and produced large berry crops (pers. obs.). In this regenerated nectar- and pollen-rich habitat, pollinator activity increased substantially, as evidenced independently by much greater fruit set in the pink lady's slipper orchid (*Cypripedium acaule*), another non-rewarding, nectarless plant at the site with an extensive long-term monitoring dataset compiled from marked individuals (Gill 1989, 1996, unpub. data). In addition, the turkeybeard floral display in these years was massive, being by far the best ever recorded in ten years of monitoring, and seed set was highly elevated compared to 1997. The pollination experiment results from 1998 and 1999 now indicated that NC flowers performed significantly better than selfed treatments for seed production, especially in 1998 when they yielded the same high numbers of seeds/fruit as both within- (WX) and between-population (BX) hand outcross treatments (**Figures 3 and 4**). Although the level of seed set in 1999 NC fruits was significantly lower than outcross treatments done on the same experimental pollination inflorescences, seed set/fruit values in other open-pollinated inflorescences not used in the pollination experiment were nearly 1 seed/fruit higher than the 1999 NC values, and thus more similar to the two 1999 hand outcross

pollination treatments (Bourg et al. unpub. ms). This discrepancy could have been due to the fact that all of the plants used in the 1999 hand pollination experiment were located on the extreme northern flank of Orchid Hill rather than distributed more evenly throughout the population and therefore may not have been visited as frequently by insect pollinators.

Furthermore, evidence of low seed production/fruit in open-pollinated plants under low flowering density conditions similar to 1997 was also obtained in the 2000 season at Orchid Hill, when only six plants, five of which were in forest burnt in 1996 and the other in undisturbed forest, produced a total of seven inflorescences in the study population (Bourg et al. unpubl. ms). These plants had an average yield of a mere 0.17 seeds/fruit in this year. While the 1996 fire may have had a negative impact on the insect pollinator community that carried into the 1997 season, it had clearly recovered by 1998 given the open pollination results in that year. Still more indication of low seed set in conjunction with low flowering densities in undisturbed habitat was gathered from two additional turkeybeard populations in 1998 and 1999 (Bourg et al. unpub. ms). These populations, approximately 2-3 km distant from Orchid Hill, set 1.7 – 2.6 seeds/fruit on average in samples of open-pollinated inflorescences. This was similar to the experimental self pollination values from 1998 and 1999 and the experimental NC values of 1999 at Orchid Hill. Therefore, when the open pollination results are considered in total along with the pollination experiment data in the context of fire, there is strong support for claiming that the dual phenomena of low flowering density Allee effects (Schaal 1978, Jennersten 1988, Kunin 1993, Lamont et al. 1993, Bond 1994, Agren 1996,

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Groom 1998, Oostermeijer et al. 1998, Kearns et al. 1998, Knight 2003) and pollinator

limitation (Bierzychudek 1981, Ashman et al. 2004) were responsible for the low open

pollination seed set in 1997 and 2000 at Orchid Hill, as well as in 1998 and 1999 in these

other populations.  Fire and its associated canopy alteration are the mechanisms by which

populations of *X. asphodeloides* are released from the reproductive deficits imposed by

the Allee effect and pollinator limitation.  This is due to the fact that fire stimulates

population-level mass flowering in both turkeybeard and other reward-producing

understory associates, which in turn attracts insects to gather nectar from these associates

as well as pollen from the copious production of the numerous, many-flowered *X.*

*asphodeloides* inflorescences.  Such facilitation of pollination by co-flowering plant

species has been suggested or noted in other systems (Rathcke 1983, Laverty 1992,

Johnson et al. 2003, Moeller 2004, 2005, Knight et al. 2005).


Although Vance et al. (2004) speculated on the role that disturbance by fire might

play in the pollination biology of *X. tenax*, their work was not conducted in the context of

a larger habitat manipulation experiment.  The results of this study on *X. asphodeloides*

agree with their characterization of *X. tenax* as a "compatible-pollen limited" herb, but

showed that turkeybeard is pollinator-limited and therefore conflict with their contention

that the congeneric beargrass is also not a "pollinator-limited" herb.   Thus the present

study contributes substantially to a better understanding of the pollination biology of the

genus under conditions of ecological perturbation.  The claim of no pollinator limitation

in *X. tenax* was based on the finding that open-pollinated inflorescences performed

significantly better than bagged inflorescences as well as the fact that prospective

pollinating insects were fairly abundant, diverse, and mostly carried only *X. tenax* pollen loads. However, their bagging experiment was done only in a single season at two sites with similar vegetation and recent disturbance histories. It is hoped therefore that the present findings for *X. asphodeloides* will stimulate multi-year comparative studies on the pollination biology of *X. tenax* in burned and unburned habitat.

In conclusion, this study has confirmed the presence of self-incompatibility in the second and only remaining unexamined species of *Xerophyllum* and provided important information for refining the phylogenetic position of the genus within the Liliales. In combination with the work of Bourg et al. (unpub. ms) it has also shown that *X. asphodeloides* is subject to pollinator limitation in years of low flowering or when populations reside in long-undisturbed, mature forest. Disturbance by fire is crucial for the alleviation of Allee effects by inducing mass flowering in turkeybeard and attracting pollinators to nectar-rewarding, co-flowering plants in turkeybeard habitat. This then facilitates cross-pollination in *X. asphodeloides* via insects that collect and feed upon the abundant pollen produced by turkeybeard inflorescences. The results of this study are important for the conservation and management of this rare species because they have shown the importance of the interaction of disturbance by fire with insect-mediated outcrossing for successful seed production in *X. asphodeloides*. In light of this, natural fires should be permitted to burn in turkeybeard habitat whenever possible to enhance reproduction and ensure long-term population viability. Prescribed fire management programs should also be developed for habitat in which permitting a natural fire to burn has become infeasible.

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**Chapter 3**

**Classification Tree and GIS-based Predictive Habitat Modeling for a Rare Fire-adapted Temperate Forest Herb**

# Classification Tree and GIS-based Predictive Habitat Modeling for a Rare Fire-adapted Temperate Forest Herb

**Abstract:**

The realms of rare species conservation and metapopulation biology theory are often interrelated, and hence share several basic challenges. Two of the most important are the critical and frequently difficult tasks of distinguishing a priori between habitat and non-habitat, and then delimiting suitable habitat patches in a study area. We combined classification tree analysis, a subset of classification and regression tree (CART) modeling, with digital data layers of environmental variables in a geographic information system (GIS) to predict suitable habitat and potential new population occurrences for Turkeybeard (*Xerophyllum asphodeloides*), a rare liliaceous understory herb associated with southern Appalachian pine-oak forests, in northwestern Virginia. Sample values from eight environmental data layers and population survey data were used in the modeling process to produce a cross-validated classification tree that predicted suitable habitat in the study area. Elevation, slope, forest type and fire frequency were the four main explanatory variables in the model. Approximately 4% of the study area was classified into five suitable habitat classes, with a misclassification error rate of 4.74%. The final 13-leaf tree correctly classified 74% of the known presence areas and 90% of the known absence areas, and ground-truthing surveys resulted in the discovery of eight new occupied habitat patches. Results of this study are important for conservation and management of *X. asphodeloides*, as well as for the applicability of the habitat modeling techniques to enhancing the study of metapopulations and disturbance regimes in

Appalachian forests. In addition, they confirm the potential and value of CART and GIS-based modeling approaches to species distribution problems. Our model was successful at defining suitable habitat and discovering new populations of a rare species at the landscape scale. Similar application to other rare species could prove very useful for addressing these and other ecological and conservation issues, such as planning transplantation or reintroduction experiments, identifying metapopulation fragmentation thresholds, and formulating conservation strategies.

**Introduction:**

The realms of rare species conservation and metapopulation biology theory are often overlapping and mutually reinforcing, yet they share several basic challenges. Two of the most important are the critical and frequently difficult tasks of distinguishing a priori between habitat and nonhabitat, and then delimiting suitable habitat patches in a study area (Hanski and Simberloff 1997). As large environmental data sets in digital format have become increasingly available in ecology in recent years, the ability to analyze landscape-level variables and to include the influence of deterministic agents in modeling of population occurrences at regional scales has become feasible. In addition, the need for statistical methods less restricted by parametric assumptions and with greater capacity for handling non-linear interactions has grown. Such analytical techniques would be particularly useful for addressing a variety of pattern and process questions in ecology.

One particularly promising analytical method is classification and regression tree (CART) modeling (Breiman et al. 1984). First used in ecology by Verbyla (1987), this technique was utilized sparingly in the ensuing decade (Borchert et al. 1989, Lees and Ritman 1991, Moore et al. 1991, Baker 1993, Michaelsen et al. 1994, Lynn et al. 1995). More recently, CART models have proven to be powerful alternatives to traditional multiple regression-based models in a number of studies. Iverson and Prasad (1998) used regression trees to replicate successfully the current distributions and predict potential future distributions of 80 eastern U.S. tree species following climate change. In a study of the distribution of three species of California oaks (*Quercus* spp.), Vayssieres et al. (2000) took advantage of an extensive historic data set to compare the predictive ability of CART models and polynomial logistic regression models, and found that CART models performed significantly better in four of the six cases considered, and equally well in the remaining two cases. De'ath and Fabricius (2000) employed regression tree models to explain from 34 – 67% of the variances in the abundances of several soft coral taxa, and compared their tree results with mixed effects ANOVA and linear regression analyses of their data. In both comparisons, they found that the tree models explained nearly identical amounts of the total sums of squares, were much better at revealing patterns in the data, and were far easier to interpret due to multiple significant higher-order interactions in the parametric analyses. On the other hand, Kintsch and Urban (2002) found that CART models based on environmental (physical) variables were not as effective at capturing rare species occurrences as a focal (indicator) species approach based on data from intense field surveys. Nevertheless, the CART method did provide an important means for reducing the number of sites requiring intensive work and finer-scale

analysis. Finally, McKenzie et al. (2000) determined that while their regression tree models explained 20-33% more of the variation in their original data than their multiple regression models, the tree-based models were more prone to extrapolation errors when applied to broader spatial scales.

In this study, we combined CART modeling with a geographic information system (GIS) to build a predictive model of suitable habitat for Turkeybeard (*Xerophyllum asphodeloides*: Liliales, Melanthiaceae) (Zomlefer et al. 2001) in the Appalachians. *X. asphodeloides* is a perennial forest understory herb that occurs in discrete mountain populations from Virginia to Alabama, as well as disjunctly in the Pine Barrens of southern New Jersey. Turkeybeard is endangered or rare in portions of its range and is in the US Center for Plant Conservation's National Collection of Endangered Plants (CPC 2004) (**Figure 1**). Despite this special status, its spatial distribution on the landscape is inadequately known, as is the extent of suitable habitat.
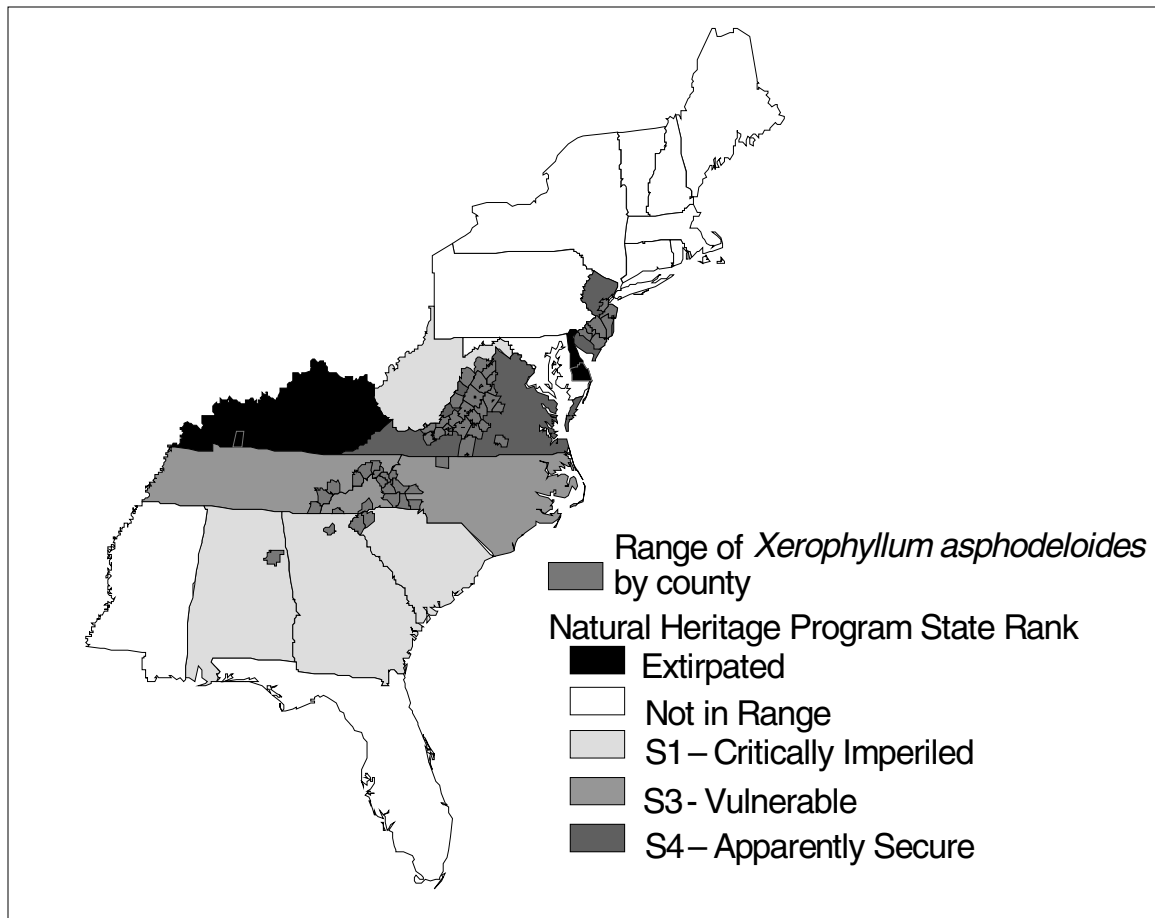
**Figure 1.** Range map for Turkeybeard (*Xerophyllum asphodeloides*) at the county occurrence level in the eastern U.S., including current NatureServe subnational/state natural heritage program conservation status rankings (NatureServe 2005).

No published studies exist addressing detailed aspects of turkeybeard's habitat preferences or distribution; however, our preliminary field observations suggested that a number of environmental landscape variables might correlate well with turkeybeard population occurrences. These included:  1) elevation – although present to some extent over the elevational range of the study area (168 – 1,360 m asl), occurrences predominated either at high elevation summits or mid-elevation slopes; 2) *slope* – populations were located mainly on either nearly flat terrain or on slightly to moderately steep slopes and spur ridges; 3) *aspect* – populations tended to occupy predominantly

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west- and north-facing sites, becoming sparse to absent as one moved onto southerly and easterly aspects; 4) *forest type* – most populations occurred in pine, mixed pine-oak and xeric oak forest types; 5) *fire history* – visible evidence of past fires were observed in most populations; 6) *perimeters* – populations were discrete and appeared to be delimited by an inability to span stream drainages and rock fields.

In addition to our observations, turkeybeard is often referred to as being a fire-adapted species dependent on disturbance by fire for its long-term population persistence (WVNHP 1994, 1995a, b; Farnsworth 2003). Anecdotal support for this assertion comes from its frequent association with fire-adapted pines in New Jersey (pitch pine, *Pinus rigida*), the Appalachians (*P. rigida* and table mountain pine, *P. pungens*), and even at its southern range limit of north-central Alabama, where its sole occurrence is in rare mountain longleaf pine (*P. palustris*) forest (Thurmond and Oberholster 1996). Its only congener, beargrass (*X. tenax*), occurs abundantly in Montana, portions of the Pacific Northwest and northern California, and southwestern Canada (Hitchcock and Cronquist 1973). There are few published studies of *X. tenax* either, but Maule (1959), Franklin and Dyrness (1973), and Hunter (1988) mention that it is often dominant in burned forest areas. Maule (1959) also concluded that the major factors influencing the distribution of *X. tenax* on Mount Rainier, Washington were elevation, slope and aspect, the last of which particularly affected soil temperature, whereas soil water content had no apparent influence. Lastly, our results from a previous fire and canopy alteration field experiment on a long-term marked *X. asphodeloides* population and assessment of fire histories at a number of population sites have shown that turkeybeard flowers massively in response to fire and that fire has occurred repeatedly in populations in recent history (unpublished manuscript).

Based on these observations and findings, we hypothesized that such environmental variables could be used in classification tree statistical analysis to identify important distributional explanatory variables, predict suitable habitat and discover new population occurrences of *X. asphodeloides*.  A lack of readily available fine-scale temperature or moisture GIS layers for the study area precluded their inclusion in our modeling effort; nonetheless, previous researchers have shown that our other variables could serve as reasonable proxies for underlying variation due to temperature or moisture gradients (Whittaker 1956, Burnett et al. 1998, Nichols et al. 1998, Kintsch and Urban 2002).

**Study Area and Methods:**

The study area consisted of the three northernmost ranger districts (Deerfield, Dry River, and Lee) of the George Washington National Forest (GWNF) in western Virginia and eastern West Virginia (lat. $37^o\ 58^{'}\ 18^{''}$ to $39^o\ 07^{'}\ 02^{''}$ N; long. $78^o\ 18^{'}\ 04^{''}$ to $79^o\ 32^{'}\ 32^{''}$ W).  The total land area was 227,216 hectares, all within the Ridge and Valley Physiographic Province (Harvill et al. 1977).

*Population surveying and mapping*

Known turkeybeard populations in the study area were surveyed by placing replicate 50- meter x 2-meter strip transects spaced at least 100 meters apart on the ground.  Three transects were done in each population except for two sites, where only two transects were surveyed due to time and size/shape constraints, respectively.  This

resulted in areal samples of 200 - 300 m$^2$ in each population. Plants were counted in five meter sections along each transect and the number of flowering individuals and inflorescences was also tallied. In addition, total direct counts of plants were conducted in two populations of small areal extent.

Mapping of the perimeter of each population was achieved by recording the surveyor's exploratory walking path with the track and waypoint functions of a Trimble Pathfinder Basic global positioning system (GPS) unit. Digital perimeter files were then downloaded and converted into polygon shapefiles for use in ArcView GIS 3.3 (ESRI 2002).

*Production of fire frequency layer*

Historical fire records were collected from GWNF ranger district offices for 158 wildfires that occurred on the study area from 1983-2000. Exact perimeters were mapped whenever available. For those records with a known size or size range and location but lacking specific perimeter maps, circles with an area corresponding to the fire acreage or mean range size were used for mapping. Only fires at least 5 acres in size were used, and both human- and lightning-caused wildfires were included in the dataset. All records were digitized onto U.S. Geological Survey digital elevation models (DEMs) of the study area. A grid consisting of 2,000 x 2,000 meter cells was overlaid onto the study area using the Coordinate Grid Maker extension of ArcView and a center point was placed in each cell. The number of fires/cell/year was then calculated for each point by summing the number of fires with any part of their perimeters entering the cell, and dividing the total by 18 years. Kriging, an advanced interpolation procedure that generates an

estimated surface from a scattered set of points, was then performed on this dataset (Isaaks and Srivastava 1989, Stein 1999, Maclean and Cleland 2003). Ordinary kriging with a 2,000-meter lag distance was used to estimate the semi-variogram, with an exponential model yielding the best fit. A thirty-meter cell size output grid was then interpolated with the Kriging Interpolator 3.2 extension to ArcView Spatial Analyst (Boeringa 2003) to yield a continuous raster layer for the study area that was suitable for use with our other data layers (**Figure 2**). The resulting fire frequency index values ranged from a low of zero fires/10 years to a high of nearly one fire/10 years.
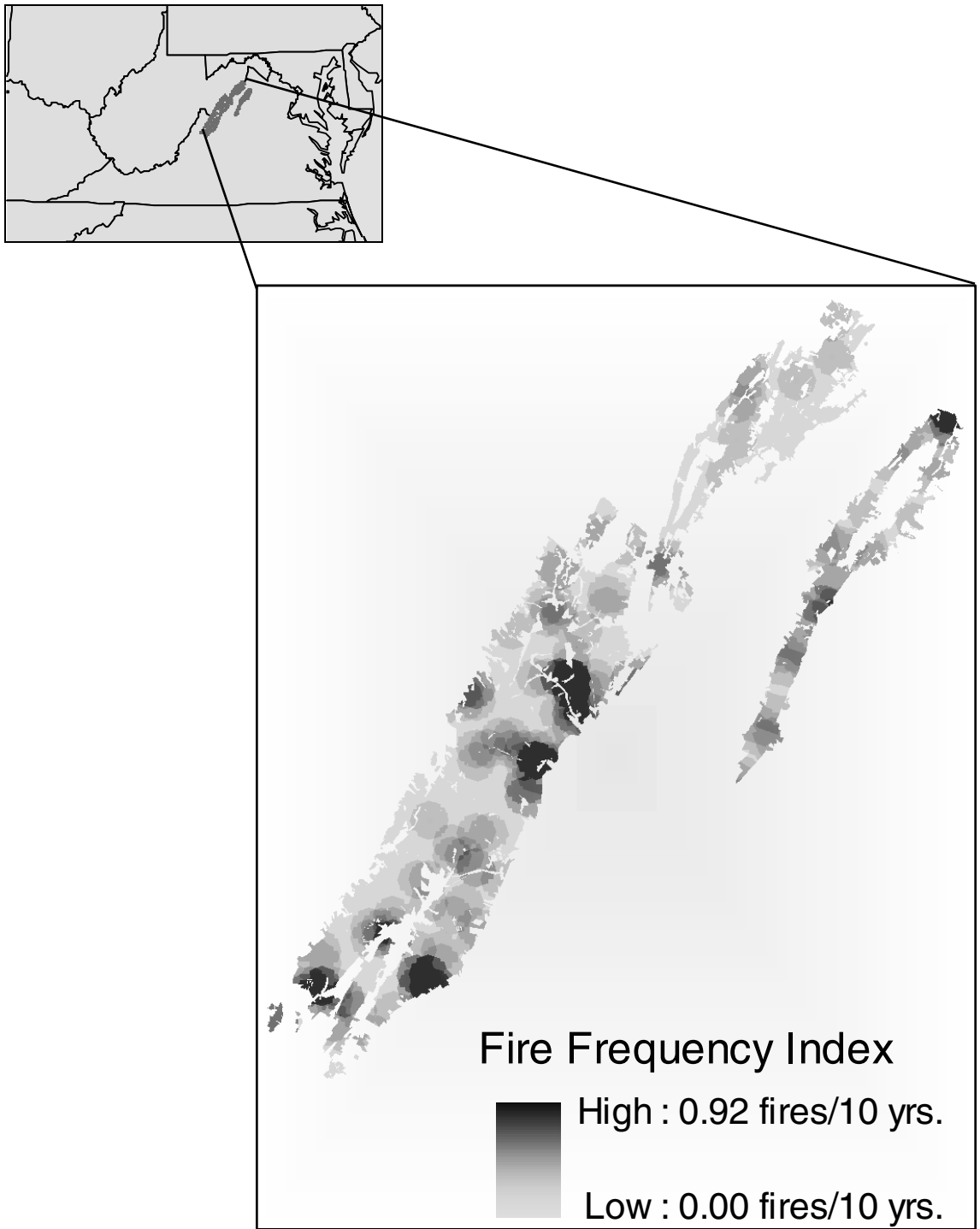
**Figure 2.** Study area location on the George Washington National Forest (inset) and kriged fire frequency raster layer for the study area, created from 158 wildfire occurrences during the period of 1983 – 2000, used in the classification tree and GIS-based predictive habitat modeling.

*Other GIS layers*

U.S. Geological Survey 30-meter resolution digital elevation models (DEMs) were gathered for the study area and merged to produce the elevation layer (USGS 1993). This layer was then employed to derive the slope, aspect, planar curvature index, and profile curvature index layers using their respective command functions in ArcInfo (ESRI 2002). The aspect layer was transformed to recalculated values aligned on a northeast-southwest axis to accord with the environmental moisture gradient, similar to the standard transformation of Beers et al. (1966). The planar curvature index describes the concavity/convexity of the land surface measured perpendicular to the aspect of the slope, while the profile curvature index describes the same phenomenon but measured parallel to the slope's aspect. Their values are unitless, with positive values indicating convexity and negative indicating concavity.

The forest type layer was a modified and condensed version of the USFS Continuous Inventory of Stand Condition (CISC) digital dataset (USFS 1996). A total of 44 CISC forest types were condensed into 9 types by grouping into broader categories, based on combining similar CISC types and grouping under the coarser-scale Southern Appalachian Assessment old growth forest types classification scheme (**Table 1**) (SAMAB 1996).

**Table 1.** Condensed forest types used in the habitat modeling effort and the corresponding Continuous Inventory of Stand Condition (CISC) type codes included in them (USFS 1996).

| Forest Type Name and Abbreviation | CISC Forest Type Codes | Percent of Study Area |
|---|---|---|
| Black Locust/Brush (BLB) | 88, 99 | 0.14 |
| Chestnut Oak/Scarlet Oak (COSO) | 52, 59, 60 | 30.45 |
| Dry-Mesic Oak (DMO) | 51, 53, 54, 55, 57 | 36.40 |
| Hemlock/White Pine/Northern Hardwoods (HWPNH) | 3, 4, 5, 8, 70, 81 | 4.18 |
| Mixed Mesophytic (MM) | 9, 41, 50, 56 | 2.65 |
| Other Conifer (OC) | 6, 7, 35 | 0.03 |
| Xeric Pine-Oak (XPO) | 10, 12, 15, 16, 20, 31, 32, 42, 44, 45, 47, 48, 49 | 21.38 |
| Pine (P) | 33, 38, 39 | 5.08 |
| Riverine/Wetland (RW) | 71, 72, 73, 75, 82 | 0.07 |

Modification and condensation of soil types from Soil Survey Geographic Database (SSURGO) digital county soil maps (NRCS 2003) was also undertaken to arrive at the final soil type GIS layer. Soil types were grouped into 7 final classes based on their similarity in six relative criteria gathered from county soil survey publications: described composition, depth, drainage, pH, fertility, and available water capacity (**Table 2**).

**Table 2.** Condensed soil classes based on SSURGO data (NRCS 2003) used in the habitat modeling effort and their descriptive rankings for the six relative county soil survey grouping criteria.

| Soil Class | Soil Type Described Composition | Depth | Drainage | pH | Fertility | Available $H_2O$ Capacity | % of Study Area |
|---|---|---|---|---|---|---|---|
| 1 | Stony/Gravelly Loams | Moderate – very deep | Moderately well - excellent | Neutral – extremely acidic | Low - moderate | Very low - moderate | 12.75 |
| 2 | Silt Loams | Very shallow – very deep | Moderately well - excellent | Neutral – very strongly acidic | Very low - moderate | Very low - moderate | 43.90 |
| 3 | Sandy/Silt/Clay Loams | Moderate - deep | Somewhat poor - poor | Alkaline - acidic | Low - moderate | Low - moderate | 0.24 |
| 4 | Sandy Loams | Moderate – very deep | Moderately well - excellent | Neutral – extremely acidic | Low - moderate | Very low - moderate | 38.70 |
| 5 | Other Alkaline/Acidic Soils 1 | Range not given | Moderately well - excellent | Alkaline - acidic | Very low - high | Very low - high | 1.57 |
| 6 | Other Alkaline/Acidic Soils 2 | Range not given | Poor | Alkaline - acidic | Moderate - high | Moderate - high | 0.02 |
| 7 | Rubble/Rock Outcrops | Moderate - deep | Excellent | Strong – very strongly acidic | Low | Low | 2.80 |

*CART model production*

A dataset for use in modeling was obtained by placing 90-meter diameter sampling circles randomly across the study area, both within and outside of mapped turkeybeard population occurrences. After elimination of those circles that either overlapped or had the majority of their area located outside the study area boundary, the final dataset consisted of 633 sample locations, 132 of which were known occupied suitable circles and 501 of which were probable absence (unsuitable) circles. Given the discrete nature and abrupt boundaries of turkeybeard populations observed in the field, as well as the fact that we had mapped all of the known locations identified either during our

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fieldwork or from consultations with natural resource managers and botanists, we felt

justified in categorizing the absence samples as such. We subsequently tested this

categorization by evaluating the model's classification accuracy on smaller known

absence areas and the known presence areas. Mean data values of each circle for each of

the eight environmental variables were extracted from their respective GIS layers with

the GIS utilities function of the ERDAS Imagine image processing software program

(ERDAS, Inc. 1997). Distribution of the data values with respect to the dependent

variable for each of the GIS layers showed that there were significant differences

between classes for all continuous variables except the landform indices, and that they

represented the actual proportions of the categories of the two discrete variables well

(**Figure 3**).
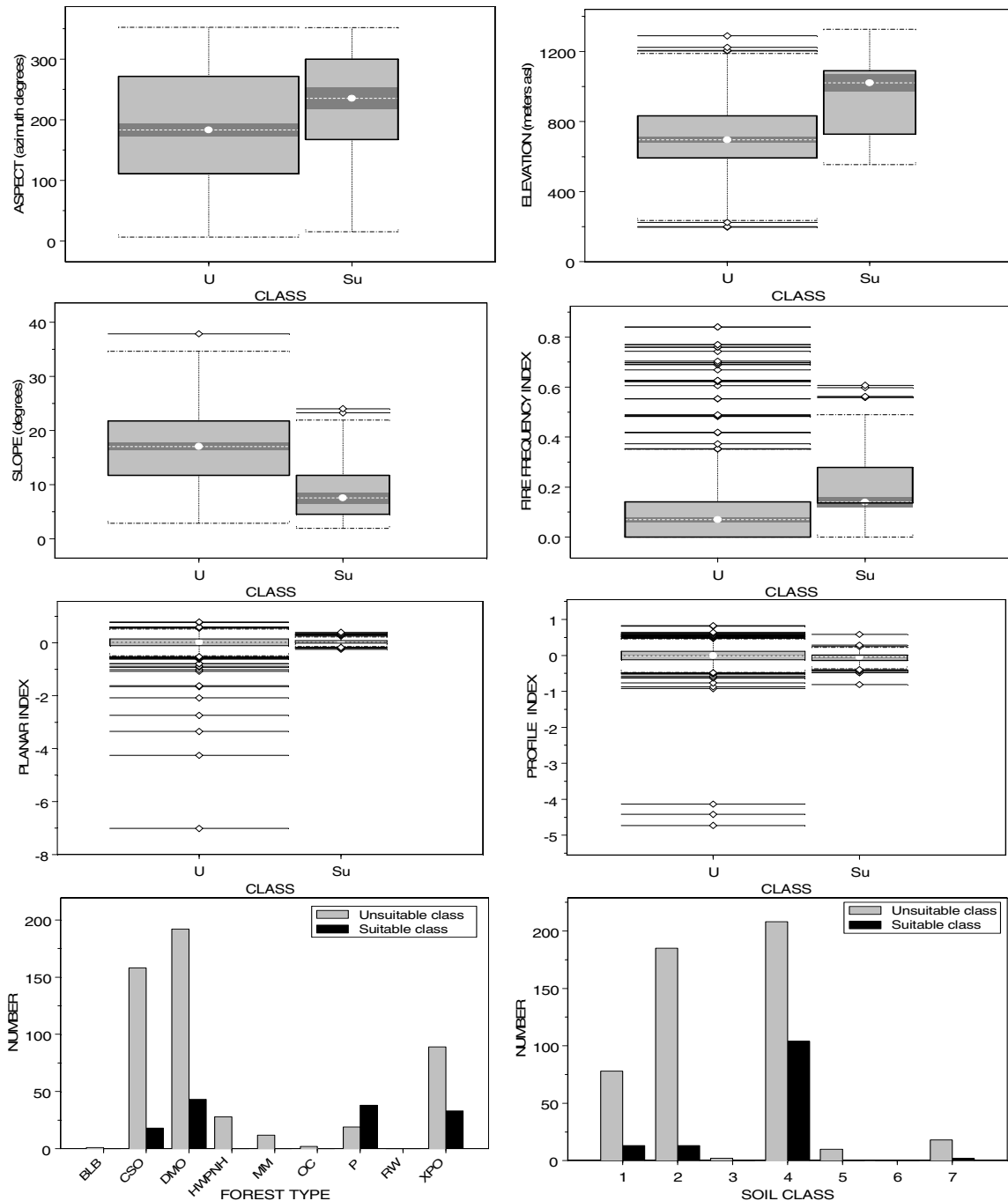
**Figure 3.** Box-whisker plots (top three rows) and bar graphs (bottom row) of the modeling dataset values for the eight environmental GIS layers with respect to the dependent variable [unsuitable (U) and suitable (Su)]. The plot of the aspect variable uses the original, untransformed values for ease of interpretation. In the box-whisker plots, the width of each box is proportional to the number of data values in each class (U - 501 samples, Su – 132 samples). The top and bottom of the boxes correspond to the $25^{th}$ and $75^{th}$ percentiles of the data values (interquartile range), the open circle denotes the median, the darker gray band within each box indicate the 95% confidence intervals, and open diamonds signify outlier values beyond the whiskers (horizontal dot-dash lines), i.e., greater than 1.5 interquartile ranges beyond the ends of each box.

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Classification tree analysis was then performed on this dataset in the S-PLUS 6.0 statistical package (Insightful Corporation 2001) using the RPART version 3 (Recursive PARTitioning, Therneau and Atkinson 1997, Mayo Foundation 2002) library addition. RPART allows one to conduct *v*-fold cross-validation runs on the data to enable the determination of the optimally sized tree, a process called pruning. We performed 10-fold cross-validation, where each run consisted of ten random divisions of the data into 90% learning and 10% test sets, using the default 'Gini' index impurity measure as the splitting index and the following control parameter settings for the fitting function: minimum number of observations in a node before attempting a split = 5, minimum number of observations in a leaf (terminal node) = 2, and the default threshold complexity parameter value = 0.001. Output from the summary function of RPART was examined to evaluate competitor and surrogate split variables. In all cases, the variable that yielded the greatest improvement to deviance was chosen as the splitting variable at a given node, and surrogate variable splits were not employed because there were no missing values for any of the dataset observations.

RPART employed the learning set to construct ten classification trees and each test set was then percolated through its respective tree to calculate a table of cross-validation error values for various tree lengths. We conducted 100 of these 10-fold cross-validation runs for a total of 1000 simulations and then tallied the optimal tree size values from their cross-validation error tables based on the two evaluation criteria of Breiman et al. (1984): the 1-SE rule and the minimum cross-validation error rule. The 1-SE rule states that the best tree is that which is smallest where its estimated error rate is within

one standard error of the minimum. The minimum cross-validation error rule states simply that the optimal tree is that which minimizes the cross-validation error in a given run. Under either rule, the modal tree size over all the simulations is then selected as the optimal tree (Breiman et al. 1984, De'ath and Fabricius 2000). This final classification tree model was then entered into the Knowledge Engineer function of ERDAS Imagine, and pixel assignment to classes for the entire study area was performed by using the resulting classification tree file along with the eight digital raster environmental layers in ERDAS Imagine's Knowledge Classifier utility.

*Model evaluation*

We evaluated the classification of the study area in two ways: 1) by calculating the percentage of known turkeybeard presence and absence areas classified correctly (i.e., included as suitable and unsuitable habitat respectively), and 2) by ground-truthing a subset of the predicted habitat patches. We digitized twenty-three small to large-sized (2,700 – 524,700 m$^2$, mean area = 108,117 m$^2$) known absence areas that we had traversed during terrain explorations in the population-mapping phase of the fieldwork to use along with the mapped known population occurrence areas for the first evaluation. For the second evaluation, we selected only those patches at least 5 hectares in size as potential ground-truthing sites, and included patches that contained known mapped turkeybeard populations. A "naïve but competent" field technician was then employed to conduct walking transect surveys through as many of these patches as possible from November 2002 – January 2003, with time, road and weather conditions permitting. By

"naïve but competent" we mean that we selected a person who was experienced in plant

surveys, plant identification, and global positioning system (GPS) use but had no prior

experience either with turkeybeard or in the study area, and did not know which patches

contained mapped turkeybeard populations beforehand.

**Results:**

Twenty-three known turkeybeard populations were surveyed and mapped during

the summer of 2000, with one additional population assessed in the summer of 2001, for

a total of 24 populations.  We found considerable range in the mean plant density, areal

extent and estimated population sizes among the populations, although the density of

plants in flower was uniformly low across all sites (**Table 3**).

**Table 3.** Plant density, areal extent, and population size estimates for the 24 mapped and surveyed populations of *X. asphodeloides* in the study area, in descending order of areal extent. [a] – densities based on direct counts; [b] – densities estimated from two 50 x 2m linear transects.

| Population | Plant Density ($\#/m^2 \pm$ SE) | Areal Extent ($m^2$) | Estimated Population Size |
|---|---|---|---|
| Rader Mtn.[b] | $0.35 \pm 0.23$ | 1,261,479 | $441,518 \pm 290,140$ |
| New Market Gap | $0.22 \pm 0.08$ | 817,208 | $179,786 \pm 65,377$ |
| Third Mtn. | $1.49 \pm 0.23$ | 305,851 | $455,718 \pm 70,346$ |
| Mud Pond Gap | $0.65 \pm 0.16$ | 261,524 | $169,991 \pm 41,844$ |
| Feedstone Mtn. | $1.47 \pm 0.58$ | 251,399 | $369,557 \pm 145,811$ |
| Rocky Run | $0.23 \pm 0.05$ | 210,020 | $48,305 \pm 10,501$ |
| Big Bald Knob | $0.86 \pm 0.04$ | 146,872 | $126,310 \pm 5,875$ |
| Dyers Knob | $0.46 \pm 0.21$ | 99,716 | $45,869 \pm 20,940$ |
| Long Run Bottom | $1.51 \pm 0.48$ | 55,185 | $83,329 \pm 26,489$ |
| Benchmark 3 | $0.45 \pm 0.06$ | 48,130 | $21,659 \pm 2,888$ |
| The Knobs | $1.16 \pm 0.45$ | 35,965 | $41,719 \pm 16,184$ |
| Benchmark 2 | $0.26 \pm 0.15$ | 35,052 | $9,114 \pm 5,258$ |
| Powerline | $0.14 \pm 0.02$ | 33,162 | $4,643 \pm 663$ |
| Narrowback Mtn. | $0.37 \pm 0.08$ | 25,702 | $9,510 \pm 2,056$ |
| Second Mtn. | $0.58 \pm 0.13$ | 18,718 | $10,856 \pm 2,433$ |
| North River | $0.36 \pm 0.16$ | 17,556 | $6,320 \pm 2,809$ |
| Black Run | $0.33 \pm 0.06$ | 17,315 | $5,714 \pm 1,039$ |
| Benchmark 1 | $0.32 \pm 0.05$ | 14,910 | $4,771 \pm 746$ |
| Orchid Hill | $0.24 \pm 0.07$ | 14,809 | $3,554 \pm 1,037$ |
| Shenandoah Mtn. 2 | $0.49 \pm 0.16$ | 7,469 | $3,660 \pm 1,195$ |
| Timber Ridge[b] | $0.38 \pm 0.08$ | 6,582 | $2,501 \pm 527$ |
| Hone Quarry Ridge[a] | 0.03 | 4,667 | 157 |
| Shenandoah Mtn. 1 | $0.47 \pm 0.05$ | 2,510 | $1,180 \pm 126$ |
| Elliot Knob[a] | 0.05 | 1,638 | 85 |
| **Mean values** | **$0.55 \pm 0.15$** | **153,893** | **$84,892 \pm 29,303$** |

Compilation of the results of the cross-validation runs yielded a 5-leaf tree as the modal size under the 1-SE rule while the minimum cross-validation error criterion produced a 13-leaf tree as the optimum (**Figure 4**). The 13-leaf tree, however, was the most frequently represented size overall, achieving moderate frequency under the 1-SE rule and scoring as the best tree in 77 of the 100 runs under the minimum cross-validation error rule. Additionally, the 13-leaf tree yielded an overall misclassification error rate of

only 4.74% when applied to the full model dataset, whereas the 5-leaf tree misclassified 7.90% of this dataset. Sensitivity (i.e., true positive rate = the proportion of observations correctly identified as suitable) of this tree size, at $0.811 \pm 0.03$, was also considerably greater than that of the 5-leaf tree ($0.652 \pm 0.04$), while specificity (i.e., true negative rate) of both tree models was high and virtually identical ($0.990 \pm 0.004$ for 13-leaf tree, $0.992 \pm 0.004$ for 5-leaf tree). Finally, use of the larger tree to classify the study area resulted in correctly classifying 74.4% of the total known presence area and 89.7% of the total known absence area, while the smaller tree was less accurate at classifying the known presence area (66.3% correct) and no better at classifying the known absence area (90.2% correct). Given these performance differences and the richer information content of the 13-leaf tree, we chose it as the optimal tree size and used it to perform the final classification of the study area (**Figure 5**). Using the misclassification error terminology of De'ath and Fabricius (2000), the 4.74% misclassification error rate of this tree compares very favorably with a 50% error rate for classification of the data based on "blind guessing" and a 20.9% error rate using the "go with the majority rule" of the null model, which in this case would constitute classifying none of the sampling circles as having *X. asphodeloides* present in them.
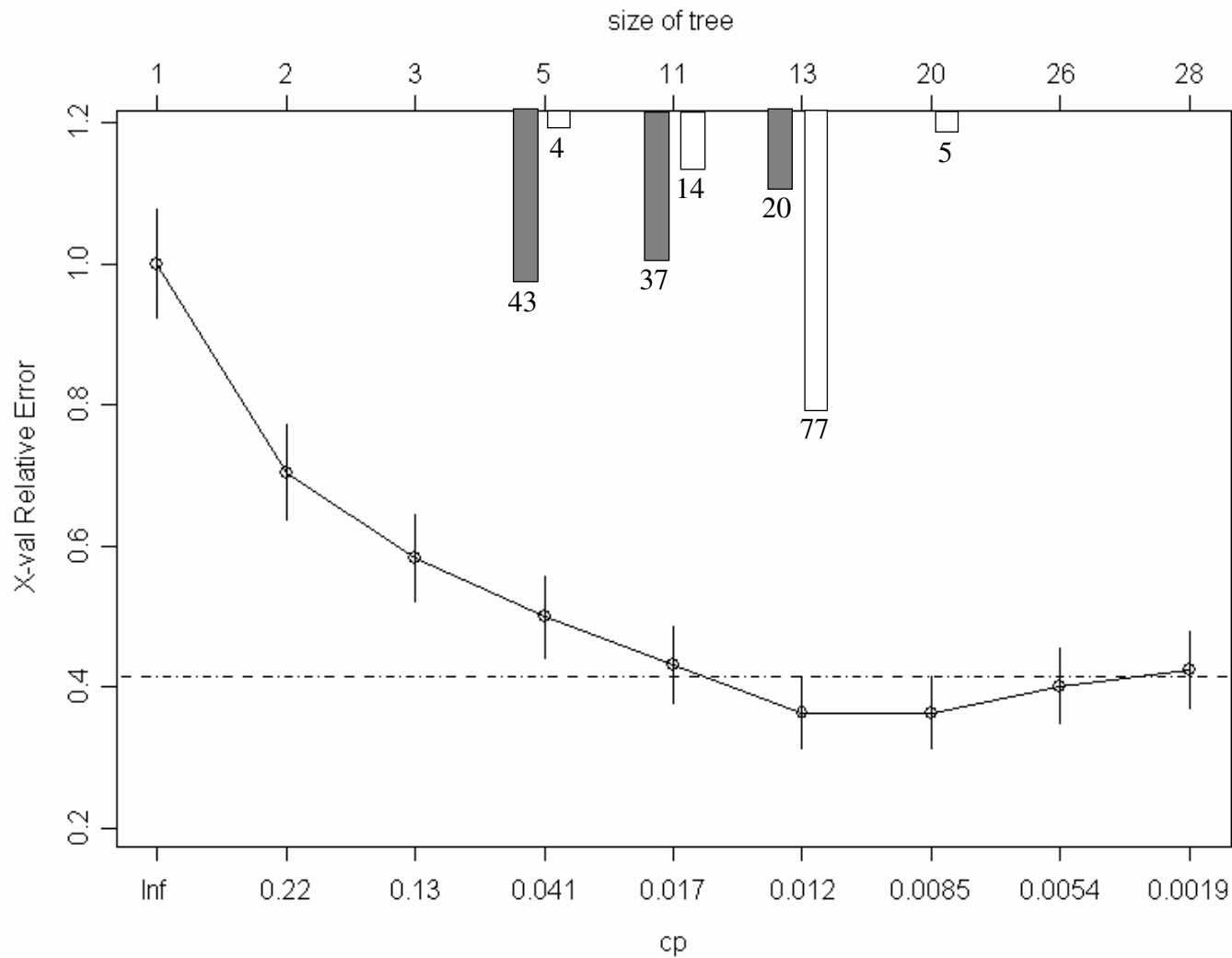
**Figure 4.** Cross-validation relative error for the classification tree modeling of *X. asphodeloides* habitat. The plot is for a single representative 10-fold cross-validation and includes 1-SE estimates for each tree size. The bar chart at the top of the plot shows the relative proportions of trees of each size selected under the 1-SE rule (gray) and minimum rule (white) from a series of 100 cross-validations. The dashed line indicates the 1-SE cut-off above the minimum error value. The bottom x-axis indicates the complexity parameter values associated with each tree size.
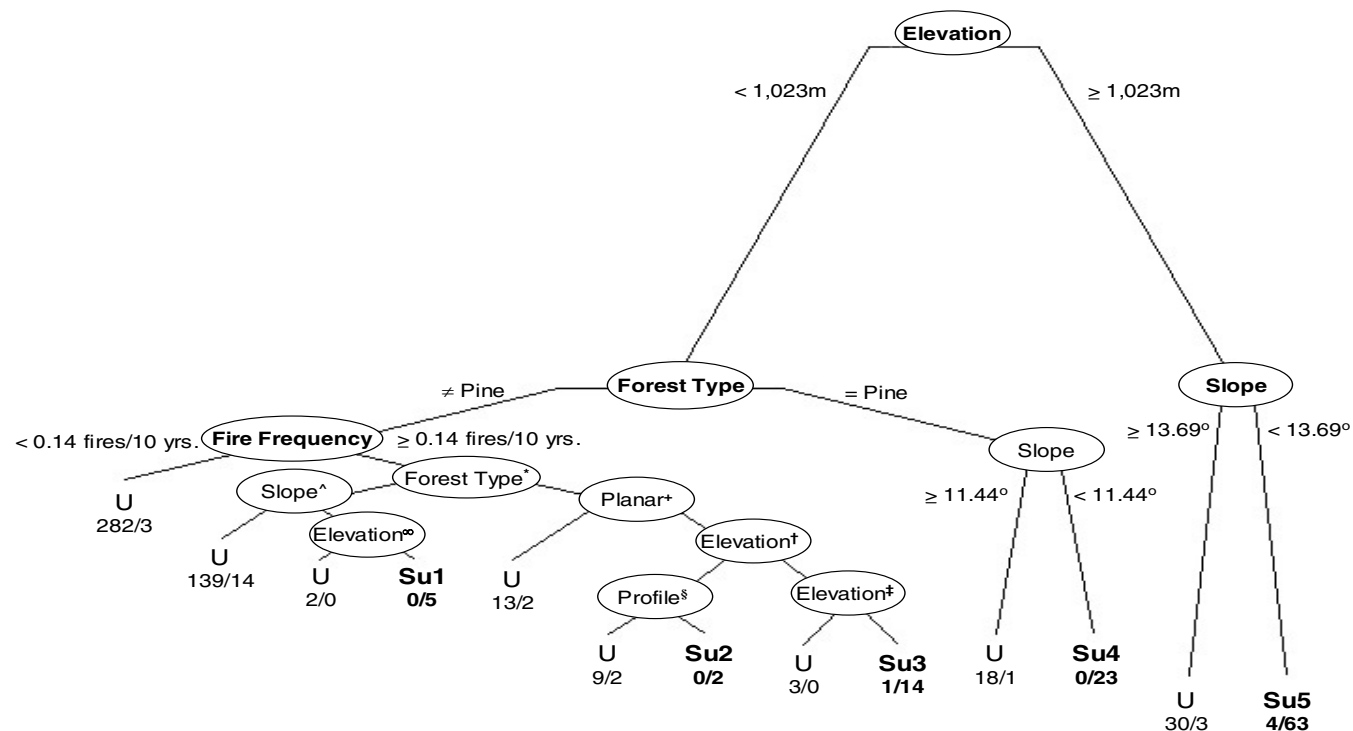
**Figure 5.** Final cross-validated classification tree that served as the basis for the model of predicted habitat for Turkeybeard (*Xerophyllum asphodeloides*) on the George Washington National Forest study area in northwestern Virginia. Splitting variables at each decision node of the tree are enclosed in ovals, and the values for each variable in the upper portion of the tree are labeled on the left and right branches emanating from each split. Values for the splits in the lower portion of the tree are as follows: [*] Forest type - left branch = COSO, DMO, HWPNH, MM, and RW; right branch = XPO, OC, and BLB (see Table 1). [^] Slope - left branch $\geq 4.55°$; right branch $< 4.55°$. [∞] Elevation - left branch $< 664$ m; right branch $\geq 664$ m. [+] Planar Index - left branch $< -0.025$; right branch $\geq -0.025$. [†] Elevation - left branch $< 742$ m; right branch $\geq 742$ m. [§] Profile Index - left branch $\geq -0.30$; right branch $< -0.30$. [‡] Elevation - left branch $\geq 876$ m; right branch $< 876$ m. Branch lengths below each split are proportional to the amount of variance explained by the classification variable at the split. The end nodes or "leaves" of the tree are labeled with the two classes of the dependent variable; **U** = unsuitable habitat, and **Su** = suitable habitat. Numbers below the end node labels refer to the number of sample points classified into that node; the first number indicates the number of 'U' samples placed into that leaf, and the second indicates the number of 'S' samples in the leaf. The five 'Su' habitat classes are in bold type and numbered (**Su1-Su5**) to correspond to the predicted suitable habitat classes in **Figure 6**.

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Application of this 13-leaf tree model to the study area resulted in placing 3.9% (8,753 ha) of the terrain into five suitable habitat classes (**Figures 5 and 6**). This tree size was most successful at achieving the multiple goals of: 1) producing a moderately-sized tree containing ecologically meaningful explanatory variables while obtaining a low misclassification error rate for the model dataset; 2) placing the highest proportion of known population areas into the suitable habitat classes while at the same time minimizing the total amount of the study area categorized as suitable; and 3) maintaining high fidelity in known absence area classification.

The final classification tree model identified the following four variables as major determinants for explaining the distribution of turkeybeard populations and identifying suitable habitat patches: elevation, slope, forest type, and fire frequency index (**Figure 5**). One hundred of 633 sampling circles in the model dataset (15.8%) occurred at high elevation (>1,023 m asl), and turkeybeard was found almost exclusively on fairly gentle slopes (<13.7$^{o}$) here. This high elevation category contained 50% (66 of 132) of the known presence sampling circles, and only three of these were misclassified. The remaining 533 sampling circles were split into two major groups by the forest type and fire frequency index variables. While only 7.9% (42 of 533) of these samples fell into pine-dominated forest types, 18.2% (24 of 132) of the known presence samples occurred here, with only one misclassified and located on more steeply sloped terrain ($\geq 11.4^{o}$). The fire frequency index variable was able to split out 285 of the final 491 samples (58%) into the very low to nil fire frequency category. Three of these were misclassified known presences, representing only 2.3% (3 of 132) of these data. The rest of the known

presence data (39 samples or 29.5%) occurred in areas of higher fire frequency ($\geq 0.14$ fires/10 years). In addition to elevation reentering into the lower branches of the tree as a classifying variable, the two measures of topographic curvature at the local scale also appeared as important factors. Suitable habitat classes in this portion of the tree model were characterized by mainly concave planar topography ($\geq$ -0.025; 18 of 132 presence samples, or 13.6%), with a small subset of these (4 of 132, or 3.0%) occurring at lower elevation sites (< 742 m asl) with some additional convexity in their profile topography. Lastly, the greatest number of misclassified samples (14 of 132 presence samples, or 10.6%) appeared in the classification node that was mainly defined as more than gently sloped areas ($\geq 4.55^{\circ}$) in predominantly deciduous forest types, where species such as *Quercus prinus, Q. coccinea, Q. rubra, Q. alba,* and to a lesser extent *Acer rubrum* were most common.

Forty-six predicted suitable habitat patches were surveyed during the ground-truthing exercises. Total distances covered in the walking transects were 54 and 69 kilometers in unsuitable and suitable habitat, respectively. Our ground-truthing technician was 100% successful (6 of 6 patches) in finding turkeybeard in those patches harboring known, previously mapped populations that were covertly included in his search list. These surveys also resulted in the discovery of eight new, occupied suitable habitat patches, equal to a 20% occupancy rate for the remaining forty ground-truthed patches (**Figure 6**). All of the five suitable habitat classes were represented at least twice in these new populations, although suitable habitat class 2 covered only a small portion (<5%) of their total area. Additionally, six false negatives were found, but these all

occurred near to predicted suitable habitat harboring known or new populations (mean

distance from nearest suitable habitat = 171 m).
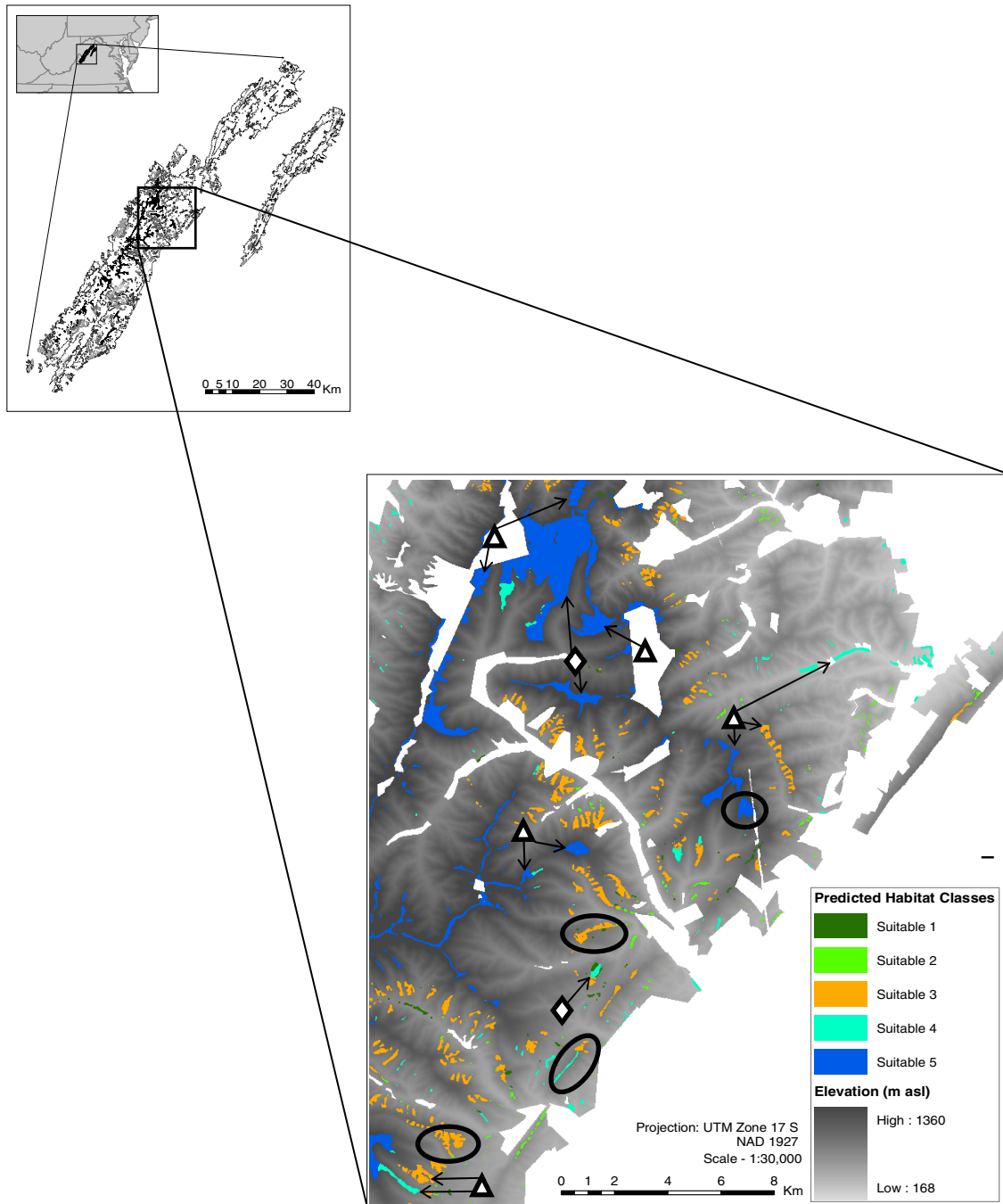
**Figure 6.** Predicted habitat model map for Turkeybeard (*Xerophyllum asphodeloides*) on the George Washington National Forest study area in northwestern Virginia (227, 216 ha, inset upper left) produced from the classification tree model. Suitable habitat color-coded categories in the magnified view correspond to the Su1 – Su5 leaves in the classification tree in **Figure 5**. Ovals encircle new population patches discovered during ground-truthing; triangles with their corresponding arrows indicate unoccupied ground-truthed patches, and diamonds with their associated arrows indicate prior known population ground-truthed patches.

**Discussion:**

Our modeling effort was successful at defining suitable habitat for and discovering new populations of a rare species in a topographically complex environment at the landscape scale. The results of our approach compare favorably with the performance achieved by CART models in several recent studies (Iverson and Prasad 1998, De'ath and Fabricius 2000, McKenzie et al. 2000, Vayssieres et al. 2000, Kintsch and Urban 2002). In addition, the model's identification of elevation, slope and fire as three of the four main explanatory variables is consistent with the findings of Maule (1959) and Franklin and Dyrness (1973) for turkeybeard's western congener, *X. tenax*. Regardless of whether elevation and slope may have served as proxies for underlying causal factors in our study, they, as well as fire frequency and forest type, played an important role in yielding a predictive model that performed well. Further investigation, GIS layer production, and model redevelopment would be needed to assess whether inclusion of other variables more directly related to factors such as temperature or moisture would improve the outcome we obtained (Vayssieres et al. 2000, Kintsch and Urban 2002).

Although we do not present evidence herein to characterize *X. asphodeloides* as having a metapopulation structure, the results are pertinent to questions of habitat definition at the metapopulation-level (Husband and Barrett 1996, Freckleton and Watkinson 2002, Murphy and Lovett-Doust 2004). Over the past decade interest in the influence of spatial structure on the ecological and evolutionary dynamics of populations has increased markedly. Indeed, advocacy for a metapopulation approach to addressing

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this issue has become extremely popular in both ecology and conservation biology (Husband and Barrett 1996, Hanski and Simberloff 1997, Hanski 1999). This is a powerful and justifiable approach because it encourages process- and scale-oriented research and conservation strategies that focus attention on among-population processes (Thrall et al. 2000). Such processes, the main examples of which are environmental stochasticity and deterministic threats like natural disturbance and succession, are the most likely ultimate causes of local population extinction (Thomas 1994, Harrison and Taylor 1997). Plants are particularly vulnerable to deterministic extinction threats due to their immobility and restricted capacity for dispersal.

In their review of 44 recent papers on the regional population dynamics of more than 33 plant species, Freckleton and Watkinson (2002) listed only two studies where potential suitable habitat was defined quantitatively (Lesica 1992, Giles and Goudet 1997). The remainders were either easily delimited (e.g., aquatic plants in transient pools), used qualitative or subjective definitions, or did not define potential habitat patches. This is not a trivial issue, as the occurrence of suitable habitat in discrete patches that may be occupied by local reproducing populations is one of the four necessary conditions for characterizing the regional dynamics of a species as a metapopulation (Hanski 1997). Our effort demonstrates a powerful and readily interpretable GIS-compatible modeling approach for satisfying this requirement in regional-level population investigations. In cases where a species does not conform as readily to suitable/unsuitable habitat delineations, predictive habitat gradient models, as

advocated by Murphy and Lovett-Doust (2004), can still be undertaken using CART modeling in combination with grid-based GIS data layers.

Our findings also have significant conservation and management implications for the role of fire in the Appalachians as well as in the life history of *X. asphodeloides* in particular. Research on fire ecology in Appalachian forest communities has traditionally focused on effects on overstory trees and their regeneration (Zobel 1969, Barden and Woods 1973, 1976; Komarek 1974, Harmon 1982, Van Lear and Waldrop 1989, Williams and Johnson 1990, Abrams 1992, Sutherland et al. 1993, Harrod et al. 1998, Shumway et al. 2001); little research has been done on the understory plant component. Fire, however, may have a major influence on the population ecology of understory species in fire-influenced communities (Bond and van Wilgen 1996, Curtis 1998, Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004). Additionally, studies of understory species such as *X. asphodeloides* are valuable, given that the Appalachian forest cover of today is almost entirely mature secondary regrowth from the extensive deforestation of the 18th and 19th centuries (Shands 1992), which obliterated much of any historical fire evidence contained in the canopy trees.

No detailed ecological studies of *X. asphodeloides* had been undertaken until this research effort. Additionally, the full extent of turkeybeard population occurrences in the Appalachians is currently unknown, constituting a critical information gap that our modeling approach can now begin to fill. *X. asphodeloides* is broadly distributed within the larger forest matrix in isolated patches across a range of drier forest types (hardwood

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to pine-dominated) that may be subject to natural succession and human-induced habitat loss. This raises the question of whether population occurrences in turkeybeard are the result of a dynamic process of individuals tracking rare patches of suitable habitat in a metapopulation context (Harrison and Taylor 1997) or whether their distribution is a relict of ancient fragmentation processes independent of edaphic and ecologically induced patchiness (Whittaker 1956). Insights into these issues and their relation to fire occurrence are particularly relevant for conservation and management of mountain populations of turkeybeard because most occur on National Forest and Park lands, where fire suppression policies have been in place for much of the past century.

Equally important, the predictive habitat modeling effort described herein has the potential for linkage to regional genetic studies through its ability to efficiently delineate and identify areas harboring new populations. Cruzan (2001) used stepwise regression models and genetic diversity data from multiple populations to estimate the critical number of neighboring populations (fragmentation threshold) and metapopulation diameter needed for the regional maintenance of genetic diversity in the large-flowered skullcap (*Scutellaria montana*). However, this was possible only because of the availability of population occurrence information from extensive and time-intensive prior field survey data collected by state resource managers. Applying our modeling approach could substantially enhance the feasibility of estimating such fragmentation thresholds for other species whose spatial distributions are poorly known. The results of this study are thus important not only for conservation and management of *X. asphodeloides* in the Appalachians, but also as confirmation of the potential and value of CART and GIS-

based modeling approaches for addressing species distribution problems and related questions in ecology.

There are some limitations to our current habitat model. First of all, as one would expect its classification accuracy decreased as population occurrence area decreased. Fifty-three percent of the known mapped small (< 5 ha) turkeybeard populations were missed by the 13-leaf tree model. Adding additional sample points from other small populations to the model dataset would likely improve classification accuracy for such areas. Secondly, the inclusion of more and better fire history data would improve the fire frequency layer and potentially lead to fire appearing as an even stronger explanatory variable in the tree model. This assertion is supported by the fact that fire frequency was the predominant splitting variable used to classify the major remaining group of misclassified presence samples (14) in the next largest tree model (15-leaf tree). We were limited to using only the most recent eighteen years of fire records because of a lack of older records covering a longer coincident time period on two of the districts of the study area. However, it appears evident that many *X. asphodeloides* sites have experienced repeated fire over at least the past 200 years, based on analyses of fire-scarred tree cross-sections collected from a subset of our turkeybeard populations on the GWNF (unpublished manuscript). It is interesting to note that even with the short time period of the available fire history data, the highest value of the fire frequency index (nearly 1 fire/10 years) corresponds well with longer-term fire frequencies (8-13 years) that have been reported for Appalachian pine and oak forest types (Harmon 1982, Abrams 1992, 2000, 2003; Sutherland et al. 1993, Shumway et al. 2001). Additionally,

the entry of the fire variable into the tree model at elevations below 1,023 meters agrees with the known patterns of lightning-caused fires on the GWNF, which occurred predominantly in the mid-elevation range (610-914 m) (USFS 1997).  Finally, application of the model to other potential study areas must be restricted to those having similar topographic, forest and soil type ranges and categories, such as those found in other parts of the southern Appalachians.  The basic modeling approach would be valid in other regions but would by necessity require testing and reevaluation in the new multivariate space.

Even though *X. asphodeloides* is a long-lived perennial and one of only two species in its genus, its distribution throughout the elevational range of the central and southern Appalachians and its relationship with fire argues against it being considered a relict species similar to a number of other Appalachian plants (Whittaker 1956, Godt et al. 1995, 1996; Kintsch and Urban 2002).  Recent work on *X. tenax* in Oregon by Vance et al. (2004) has shown that this species has an early-acting self-incompatibility system, and our own pollination studies of *X. asphodeloides* have documented a similar self-incompatible breeding system (unpublished data).  This suggests that in the longer term, populations may be vulnerable to deterministic extinction brought about by natural succession and persistent low flowering levels in the absence of fire, given the present altered fire regimes in the Appalachians.  If periodic fire enables population maintenance and enhances the potential for occasional gene flow among populations, then there may be validity in characterizing turkeybeard's population dynamics as a "habitat-tracking

metapopulation" (Harrison and Taylor 1997).  Additional research is needed to fully evaluate this hypothesis.

Our modeling effort was successful at defining suitable habitat and discovering new populations of a rare species at the landscape scale.  The model is relevant to metapopulation-level questions, and has potential for linkage to population genetic studies.  Application of similar modeling efforts to other rare species could be very useful for defining suitable habitat, discovering new populations, planning transplantation or reintroduction experiments, identifying metapopulation fragmentation thresholds, and addressing a variety of other ecological and conservation questions.

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