

Spatial and temporal optimization in habitat placement for a threatened plant: the case of the western prairie fringed orchid

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Abstract

This paper investigates an optimization approach to determining the placement and timing of habitat protection for the western prairie fringed orchid. This plant's population dynamics are complex, creating a challenging optimization problem. The sensitivity of the orchid to random climate conditions is handled probabilistically. The plant's seed, protocorm and above-ground stages are all accounted for in a case example from the Sheyenne National Grassland in North Dakota. Sensitivity of the case example model to dispersal assumptions and climate condition probabilities is demonstrated. © 1999 Published by Elsevier Science B.V. All rights reserved.

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1. Introduction

Spatial patchiness is a common feature of the distributions of most plants, particularly those occurring in ephemeral habitats (e.g. Schemske et al., 1994). This factor, combined with their immobility through certain stages of life, make plants seem particularly appropriate for spatial landscape analyses. However, a surprisingly small

number of studies have examined plant populations with such an approach, particularly in terms of testing theoretical models (Husband and Barrett, 1996; Wu and Levin, 1997). Plant population dynamics differ from those of animals in a number of ways, including vulnerability levels independent of the size and age of populations (e.g. Husband and Barrett, 1996) and the role of seed dormancy in maintaining populations (e.g. Kalisz and McPeck, 1993). A potential outcome of these factors, especially in ephemeral habitats like wetlands, is that local changes in habitat conditions

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can cause drastic reductions in population size and distribution; but the presence of a viable seed bank can save the species from extinction. One of the challenges, then, in developing conservation strategies for rare plants, is to develop plans that account for the influence of climatic conditions and seed viability and dispersal through time on colonization and extinction rates of local populations (Malanson, 1996; Malanson and Armstrong, 1996; Valverde and Silvertown, 1997).

This paper explores the possibility of using an optimization modeling approach to maximize a plant species population by strategically selecting the placement and timing of protected plant habitats, using a threatened wetland species as an example. Optimization has traditionally been applied to economic problems, but shows promise in ecological problems such as habitat protection because efficiency is important, given the limited amount of habitat that can be protected (Nevo and Garcia, 1996; Tiwari et al., 1996; Batabyal, 1998). Optimization methods are applicable when it is desired to get as much (or as little) of something as possible given limited resources (Hof and Bevers, 1998).

The western prairie fringed orchid (*Platanthera praeclara* Sheviak and Bowles) was once distributed throughout the wetlands west of the Mississippi River in the tallgrass prairie of the central United States and southern Canada. With the conversion of prairie to crop land and the encroachment of other human development, much of the original habitat has been lost. Concern about the limited number of populations and their relative isolation led to federal listing of the species as threatened (US Fish and Wildlife Service, 1989). Populations of *P. praeclara*, referred to as “the orchid” hereafter, are restricted to the Great Plains States and Manitoba; the three largest metapopulations occur in Minnesota and North Dakota in the United States and in southern Manitoba in Canada (US Fish and Wildlife Service, 1996).

The orchid metapopulation in North Dakota is centered on the Sheyenne National Grassland and nearby roadside ditches and private lands in the southeastern corner of the state (US Fish and Wildlife Service, 1996). Within this area, the or-

chid has a patchy distribution that appears to be the result of the distribution of wetland swales on the landscape, its dispersal ability and water table fluctuations in response to climatic conditions. Excessive drought or flooding can cause local population decline and extinction (Sieg and King, 1995). Available data (discussed below) suggests that the presence of seeds at sites with adequate moisture allows the re-establishment of those local populations. In this manner, the metapopulation shifts in time and space in response to the dynamics of the water. In addition, the orchid is threatened by habitat conversions such as plowing on non-public land and by ill-timed mowing, grazing, burning, water table manipulation and other management activities on both public and private lands (US Fish and Wildlife Service, 1996). When it is possible to protect orchid habitat from these activities and uses, the problem of locating that protection over time remains. This is a natural problem for optimization methods. Capturing the population dynamics of a complex plant like the orchid in an optimization model is challenging, however, so this is an exploratory study. We will use discrete time periods and difference equations to capture these dynamics with linear constraints (in a linear program), thus allowing solution to large problems with standard simplex algorithms. We will begin by summarizing the population dynamics we wish to capture and then proceed to the model formulations.

2. Population dynamics

The orchid is a perennial plant characterized by erratic above-ground growth and flowering. Periods of high numbers, usually linked with above-average precipitation, are followed by years when the orchids have seemingly disappeared (Bowles et al., 1992). The orchid has three distinct stages that we will model: seeds, protocorms and above-ground plants. Little is known about seed dispersal in this species. Orchid seeds may be wind-dispersed (Bowles, 1983), but their minute size, air-filled testa, water-repellent lipoid layer and buoyancy, make them well-equipped for water dispersal (Rasmussen, 1995). In our model, we

assume that the seeds disperse exclusively by water (flooding). Thus, seed dispersal, as well as carrying capacity, seed production, survivability and other population dynamics of the orchid, are all strongly influenced by yearly climate condition. We will define discrete climate conditions and then optimize the placement of orchid habitat based on expected values across those climate conditions. This approach requires some explanation before proceeding.

Information on the population dynamics of the orchid is rather limited, but perhaps the most telling observation occurred recently on the Sheyenne National Grassland. The orchid recovered quite dramatically beginning in 1992 (a wet year) after 5 relatively dry years, in which above-ground orchid populations had dwindled to very low numbers (Sieg and King, 1995). It is unlikely that this recovery can be attributed to plants returning from dormancy because recent demographic data collected on the Sheyenne National Grassland indicate that most above-ground plants live three years or less and once absent, the odds of them remaining absent the following year are 80% or more (Sieg and King, 1995). An alternate explanation for this recovery is the presence of a seed bank with at least some viable seeds persisting through the drought years. From this observation, we conclude that the orchid seeds (and thus the orchids themselves) do not seem to be subject to catastrophic loss from a single or even a string of 'bad' years. The effects of seed production and dispersal last long enough (in terms of their viability) that we can expect the 'good' years to compensate for 'bad' years. By this logic, we would be more concerned with maximizing the long-term mean population levels under protection and less concerned by yearly population fluctuations, so long as we take the viability and dispersal of the seed bank into account.

We make the following assumptions about the orchid population dynamics with each year defined as the calendar year from January to December. Seeds that have accumulated are subject to transport, regardless of age, during wetter years when flooding occurs.

1. Seeds are not produced until late in the year (September) and do not germinate until, at the earliest, the next spring.
2. Germinated seeds spend a year underground as protocorms and emerge the next year (with a given success rate) as 'above-ground' plants. This assumption is based on in situ germination trial data collected in 1995 and 1996 on the Sheyenne National Grassland (Richardson et al., 1997).
3. A predictable portion of the above-ground plants flower each year yielding a constant reproductive (seed production) rate per plant.
4. Seeds remain viable at a decreasing rate (fixed% loss per year) over a number of years.
5. During dry years, no seed transport occurs at the scale of our model.
6. During wetter years, when flooding occurs, seed transportation takes place in the spring, before the production of that year's seeds. Germination takes place after transport, but again only applies to seeds produced in previous years.
7. Different areas have different orchid carrying capacities depending on yearly climate, determined mostly by topography.
8. Seed production, seed viability, germination rates, protocorm emergence rates and plant survival rates are all a function of the climate condition in the year the rates are applied, not climate conditions in previous years. We recognize that this simplifying assumption may ignore the influence of climate condition in late summer on the formation of the perennating bud.

The landscape where the orchid appears is typically rolling grassland with swales and hummocks as the primary distinguishable topographic features. Orchid habitat in different climate conditions and seed dispersal through different flooding conditions are largely determined by this swale-hummock topography, so we will characterize the spatial variables in our model by 'swale complexes'. Each complex includes multiple 'contours'—areas of different elevation that surround the deepest contour which is the lowland of the given swale. Little is known about the actual seed dispersal process during the wetter years that

produce flooding. In the case example, we will investigate two sets of assumptions which bracket the possibilities that seem reasonable. It is assumed that no seeds leave or enter the given study area from the outside, creating a closed system for modeling purposes. Thus, in a real world application, the study area should be defined by the limits to flooding-caused seed dispersal as determined by topography and climate conditions included.

We define the following indexes, variables and parameters for use throughout the paper:

Indexes

i and h	index swale complexes
j and k	index contours within a swale complex
t	indexes time
w	indexes climate conditions

Variables

S_{ijt}	the expected above-ground plant population in swale i , contour j and time t
D_{ijt}	the expected number of viable seeds in swale i , contour j and time period t
B_{ijt}	the expected protocorm plant population in swale i , contour j and time t
Y_{ijt}	the area in swale i and contour j , protected for orchids in time period t

Parameters

N_{ij}	the initial value for S_{ijt}
M_{ij}	the initial value for D_{ijt}
L_{ij}	the initial value for B_{ijt}
p_w	the probability of climate w occurring in any given year
v_{ijw}	the proportion of seeds that do not germinate but remain viable for possible future germination in swale i , contour j , climate w , in any given year
g_{ijw}	the proportion of seeds that germinate in swale i , contour j , climate w , in any given year

r_{ijw}	the number of seeds produced per above-ground plant in swale i , contour j , climate w , in any given year
u_{ijkw}	the proportion of seeds, from swale h and contour k that, when connected to swale i and contour j by climate condition w , will settle in swale i and contour j
q_{ijw}	the success rate of germinated seeds becoming protocorms in swale i , contour j and climate w in any given year
f_{ijw}	the rate at which protocorms survive and emerge as above-ground plants in swale i , contour j and climate w , from 1 year to the next
z_{ijw}	the survival rate of above-ground plants in swale i , contour j and climate w , from 1 year to the next
c_{ijw}	the above-ground plant carrying capacity in swale i , contour j and climate w in any given year
A_{ij}	the area in swale i , contour j
$\bar{Y}$	a policy-driven limit on the total amount of orchid habitat that can be protected for orchids
a_{ijw}	the protocorm carrying capacity in swale i and contour j and climate w in any given year

The orchid population dynamics all imply non-linear relationships over time, but such relationships can often be captured in linear constraints by using difference equations and discrete time periods. For example, take a simple exponential growth function (ignoring habitat or other limits):

$$S(t) = S(0)e^{rt}$$

taking the derivative with respect to time yields:

$$\frac{dS}{dt} = rS(0)e^{rt} = rS(t)$$

which means that with discrete time periods, $S_{(t+1)}$ is related to S in the previous time period (S_t) by:

$$S_{(t+1)} = r \cdot S_t \quad (1)$$

To capture the orchid population dynamics with difference equations like (1), we begin by setting initial conditions for the above-ground population, viable seed numbers and protocorm population:

$$S_{ij0} = N_{ij} \quad \forall i, \forall j \quad (2)$$

$$D_{ij0} = M_{ij} \quad \forall i, \forall j \quad (3)$$

$$B_{ij0} = L_{ij} \quad \forall i, \forall j \quad (4)$$

The viable seed numbers in subsequent time periods are determined by:

$$D_{ijt} = \sum_w p_w \left[\sum_h \sum_k e_{ijhkw} (v_{hkw} \cdot D_{hkt(t-1)} + r_{hkw} \cdot S_{hkt(t-1)}) \right] \quad \forall i, \forall j, t = 1, \dots, T \quad (5)$$

Note: $e_{ijhkw} = 1$ if swale $h = i$, contour $k = j$ and contour j is not flooded by climate w
 $= u_{ijhkw}$ if climate w connects swale i and contour j with swale h and contour k
 $= 0$ otherwise

Eq. (5) determines the viable seed numbers in all subsequent time periods, based on the previous year's population (and the seed production from it) and the surviving viability of previously-produced seeds. The different climate conditions and dispersal occurring in them, are accounted for probabilistically in Eq. (5). The e_{ijhkw} coefficients are defined so as to correctly account for all seeds in any given time period.

The protocorm populations in subsequent years are determined by:

$$B_{ijt} \leq \sum_w p_w [(q_{ijw} g_{ijw}) \cdot D_{ij(t-1)}] \quad \forall i, \forall j, t = 1, \dots, T \quad (6)$$

$$B_{ijt} \leq \sum_w p_w [a_{ijw} A_{ij}] \quad \forall i, \forall j, t = 1, \dots, T \quad (7)$$

The protocorm population in each area, in each time period after the initial one, is determined by whichever of (6) or (7) is binding (is the limiting factor). Inequality (6) limits the protocorm population by the germination and success rate of seeds becoming protocorms. Inequality (7) limits the protocorm population by the space limits (carrying capacity) of the habitat area.

The above-ground populations in subsequent years are determined by:

$$S_{ijt} \leq \sum_w p_w [f_{ijw} \cdot B_{ij(t-1)} + z_{ijw} S_{ij(t-1)}] \quad \forall i, \forall j, t = 1, \dots, T \quad (8)$$

$$S_{ijt} \leq \sum_w p_w [c_{ijw} Y_{ijt}] \quad \forall i, \forall j, t = 1, \dots, T \quad (9)$$

The above-ground population is determined by whichever of (8) or (9) is limiting. Inequality (8) limits the above-ground population by the survival rate of existing plants and the emergence rate of the protocorms becoming above-ground plants. Inequality (9) limits the above-ground population by the carrying capacity of the habitat area.

In addition, we include:

$$Y_{ijt} \leq A_{ij} \quad \forall i, \forall j, t = 1, \dots, T \quad (10)$$

$$\sum_i \sum_j Y_{ijt} \leq \bar{Y} \quad t = 1, \dots, T \quad (11)$$

Inequality (10) limits the areas allocated to orchid habitat to the areas available. And, inequality (11) limits the total amount of orchid habitat allowed—a policy constraint.

3. Case example

3.1. Formulation

In the model that we built to demonstrate these formulations, we had to make some specific assumptions. First, we assumed that the v , r , g , q , f , a , z and c parameters only vary by the contour and climate conditions, but not individual swale

complexes, thus allowing us to drop the i subscript from those parameters.

Second, we assume that we only have three discrete climate conditions: a ‘dry’ condition (indexed ‘1’) that represents drought or near-drought conditions, a ‘mid’ condition (indexed ‘2’) that allows some water-based dispersal of seeds and a ‘wet’ condition (indexed ‘3’) that disperses seeds with flooding out to the limits of the orchid habitat. We also assume three contours for each swale complex: a ‘deep’ contour (indexed ‘1’) that delineates the orchid habitat during the dry climate condition, a ‘medium’ contour (indexed ‘2’) that delineates the extent of seed dispersal in the mid climate condition and a ‘high’ contour (indexed ‘3’) that delineates the extent of the area that is potential orchid habitat under any climate condition. During the dry climate condition, again, only the deep areas have any appreciable orchid habitat. During the mid climate condition, the deep and medium contours are good orchid habitat, but diminished habitat carrying capacity occurs in the high contour. During the wet climate condition, the carrying capacity in the deep contour is diminished by deep flooding, but the medium and high contours are good orchid habitat.

Third, we assume (initially) that seed dispersal over whatever area is flooded by a given climate condition is random, mixing all seeds and placing them uniformly throughout the affected areas when the waters recede and the seeds settle out on the ground. This preserves the correct number of seeds and allows us to calculate expected seed dispersal coefficients based on area alone. A formulation for these specific assumptions is:

Maximize:

$$\sum_i \sum_{j=1}^3 \sum_t S_{ijt} \quad (12)$$

Subject to:

$$S_{ij0} = N_{ij} \quad \forall i, \forall j \quad (13)$$

$$D_{ij0} = M_{ij} \quad \forall i, \forall j \quad (14)$$

$$B_{ij0} = L_{ij} \quad \forall i, \forall j \quad (15)$$

$$\begin{aligned} D_{ijt} = & p_1(v_{j1} \cdot D_{ij(t-1)} + r_{j1} \cdot S_{ij(t-1)}) \\ & + p_2 \left[\sum_h \sum_k e_{ijk2} (v_{k2} \cdot D_{hk(t-1)} + r_{k2} \cdot S_{hk(t-1)}) \right] \\ & + p_3 \left[\sum_h \sum_k \frac{A_{ij}}{\sum_{h'k'} A_{h'k'}} (v_{k3} \cdot D_{hk(t-1)} + r_{k3} \cdot S_{hk(t-1)}) \right] \end{aligned} \quad (16)$$

$\forall i, \forall j, t = 1, \dots, T$

$$\begin{aligned} e_{ijk2} = & X_{ih} \frac{A_{ij}}{\sum_{h'} X_{ih'} \sum_{k'=1}^2 A_{h'k'}} \text{ for } j = 1, 2 \text{ and } k = 1, 2 \\ = & 1 \quad \text{for } j = 3, k = 3, i = h \\ = & 0 \quad \text{otherwise} \end{aligned}$$

$X_{ih} = 1$ if the No. 2 contours of swale i and h are connected by condition 2, including when $i = h$, 0 otherwise

$$B_{ijt} \leq \sum_w p_w [(q_{jw} \cdot g_{jw}) \cdot D_{ij(t-1)}] \quad \forall i, \forall j, t = 1, \dots, T \quad (17)$$

$$B_{ijt} \leq \sum_w p_w [a_{jw} A_{ij}] \quad \forall i, \forall j, t = 1, \dots, T \quad (18)$$

$$\begin{aligned} S_{ijt} \leq & \sum_w p_w [f_{jw} \cdot B_{ij(t-1)} + z_{jw} S_{ij(t-1)}] \\ & \forall i, \forall j, t = 1, \dots, T \end{aligned} \quad (19)$$

$$S_{ijt} \leq \sum_w p_w [c_{jw} Y_{ijt}] \quad \forall i, \forall j, t = 1, \dots, T \quad (20)$$

$$Y_{ijt} \leq A_{ij} \quad \forall i, \forall j, t = 1, \dots, T \quad (21)$$

$$\sum_i \sum_j Y_{ijt} \leq \bar{Y} \quad t = 1, \dots, T \quad (22)$$

All variables and parameters (other than X_{ih}) are defined as before, except for the omission of the i subscript from the parameters previously indicated. The objective function (12) maximizes the expected above-ground orchid population totaled across all habitat areas and time periods. All time periods are included to reflect a concern for all years in the planning time horizon (including a recovery process), but other objective functions could also be used.

In order to bracket the reasonable possibilities for seed dispersal under flooding conditions, we also examine a more conservative set of dispersal assumptions in Equation set (16). This alternative is formulated by setting all:

$$X_{ih} = 1 \text{ if } i = h, = 0 \text{ otherwise} \quad (23)$$

and by replacing the third term (for climate condition 3) in (16) with:

$$p_3 \cdot \left[\frac{\sum_h \sum_k \frac{A_{ij}}{\sum_{j'} A_{ij'}} \lambda_{ih} (V_{k3} \cdot D_{hk(t-1)} + r_{k3} \cdot S_{hk(t-1)})}{\sum_{j'} A_{ij'}} \right] \quad (24)$$

Where:

$$\lambda_{ih} = \frac{\gamma_{ih}}{\varnothing_h} \text{ if } i \neq h, = 1 - \left(\sum_{h' \neq i} \alpha \frac{\gamma_{ih'}}{\varnothing_i} \right) \text{ if } i = h \quad (25)$$

$\gamma_{ih}, \gamma'_{ih}$	the length of the common border between swale complex i and swale complex h (or h')
$\varnothing_i, \varnothing_h$	the perimeter of the (source) swale complex h (or i)
α	the proportion of seeds that would exit swale complex h in climate condition 3, if there were no impediments anywhere around its perimeter

Equation set (23) assumes that, under climate condition 2, no inter-swale complex seed dispersal takes place—only seeds within each swale complex are mixed across the contours contained in that swale complex. In (24) and (25), under climate condition 3, seeds are only exchanged between adjacent swale complexes. These exchanges take place as a linear function of the ratio of common perimeter to total perimeter (of the source cell). They are also scaled by the α parameter that indicates the proportion of seeds that would disperse if the entire perimeter of the source swale complex is common with some other swale complex (as opposed to non-habitat areas including areas outside the study area boundary). This formulation assumes

a tendency of the seeds to disperse in a 360° pattern, with seeds staying in the source swale complex if hindered by the topography of the non-habitat areas (hummocks). All of the seeds within each swale complex, including those that enter from an adjacent swale complex, are again randomly mixed across the relevant contours under climate condition 3. If it was desired, the α parameter could vary according to the source swale complex, to account for source swale size or other special properties, but we will assume it to be a constant.

3.2. Landscape

Fig. 1a shows an enhanced graphic of the selected study area, a 300 ha square located in the Sheyenne National Grassland in southeastern North Dakota. The topographic data were obtained from the United States Geological Survey EROS Data Center in Sioux Falls, South Dakota (US Geo Data Digital Elevation data). These data classify 7.5 min land units into discrete elevation classes defined in feet, so we retain those units. On the basis of this landscape and observed flood conditions, the three contours were identified by the color-codes indicated. The deepest areas (contour 1) are coded blue, the middle ground (contour 2) are coded light green and the highest habitat areas (contour 3) are coded dark green. The yellow and orange areas are hummocks and are designated as non-habitat. This graphic was also used to delineate 22 swale complexes as shown in Fig. 1b. As is evident, several of the swale complexes do not have the lowest contour (number 1), but all have the other two. All area, perimeter and common border calculations were performed with the same GIS software that produced these graphics (ARC/INFO). With the initial seed dispersal assumptions, the third (wettest) climate condition floods and connects all of the area contained by the dark green contour, also, the second climate condition will connect the middle (light green) contour areas for swales 1, 2 and 3, for swales 13, 14, 15 and 16 and for swales 20 and 21. With the conservative seed dispersal

assumptions, the wettest climate condition connects only the adjacent swale complexes and the mid climate condition will only mix the seeds within each swale complex.

3.3. Parameters

For demonstration purposes, we wanted to model a situation where past management practices have created a loss in orchid populations and the modeling effort is utilized as an aid in developing a strategy to identify critical habitat

for protection. Thus, we assumed initial presence of above ground plants and protocorms to be limited to swale complex 2. The initial density of above ground plants in this swale complex was assumed to be one-half the average carrying capacity (across climate conditions). The initial density of protocorms was assumed to be one-fourth the average protocorm carrying capacity. And, it was assumed that initial seed density was 10 000 seeds/ha in swale complex 2 and 100 seeds/ha for all other habitat areas.

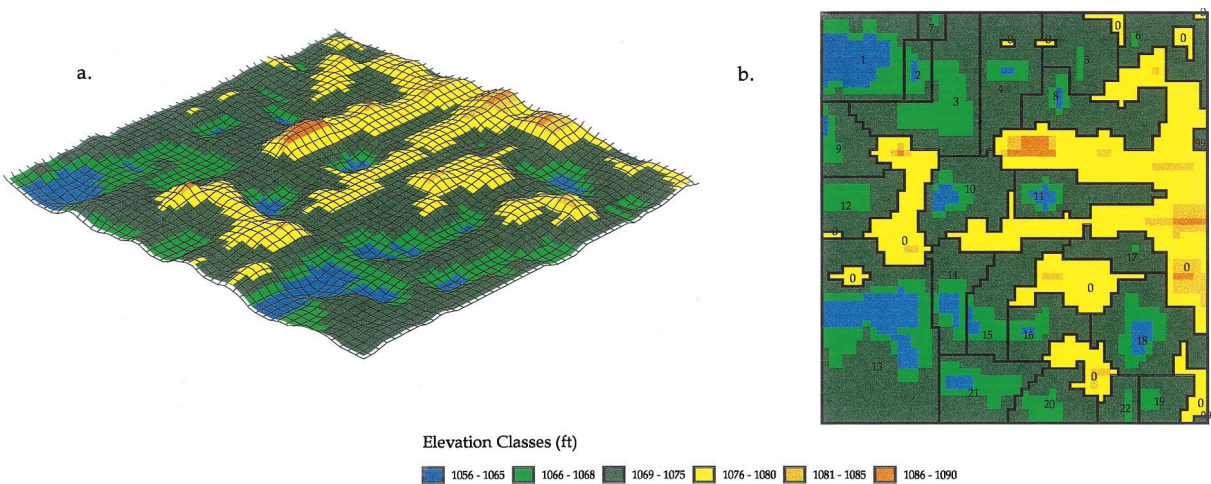


Fig. 1. Landscape of the case study area (a) and the delineation of numbered swale complexes (b).

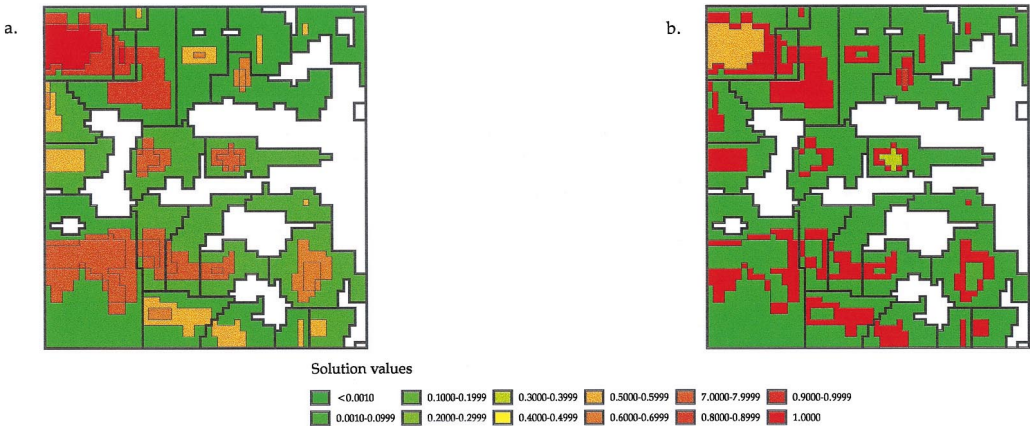


Fig. 2. Area allocated to orchid habitat (white areas are non-habitat) in the base solution with initial seed dispersal assumptions in time period 16 (a) and in time period 20 (b).

The climate condition probabilities were difficult to estimate because the relationship between climate indicators such as precipitation and on-the-ground conditions is lagged and indirect. We were able to obtain unpublished ground water (well) data from the US Geological Survey for two wells in the area for the years 1976–1997. These ground water data are more directly related to orchid habitat conditions than are precipitation records, but 21 years are obviously inadequate to provide a statistically valid estimate of the desired probabilities. These data do provide a rough estimate, however, for use in our demonstrative model. The data from one of the wells indicated 8 years (1976, 1979, 1984, 1986, 1993–1996) that we could associate with wet years in terms of orchid habitat, where the ground water peaked within $2\frac{1}{2}$ feet of the surface. Treating these as the wet years in the historical data suggests a probability of 8/21 (0.381) for condition 3. From Fig. 1a, the middle contour is about 3 feet deep, so we counted the years with peak ground water depths between $2\frac{1}{2}$ and $5\frac{1}{2}$ feet as years with climate condition 2—there were seven of them implying a probability of 7/21 (0.333). The remaining years, where the well's ground water depth did not get within $5\frac{1}{2}$ feet of the surface, were treated as climate condition 1 years, with a probability of 6/21 (0.286). The data from the second well were similar, except they did not indicate 1984 as a wet year. To demonstrate the sensitivity of the model to these probabilities, we tried this adjustment,

discussed further in the Results section.

The other parameter values are given in Table 1. These parameters, under the various scenarios, are based on published and unpublished data collected on the Shenyenne National Grassland beginning in 1987. All unpublished data are on file at the Rocky Mountain Research Station, Rapid City, SD.

Our estimation of the proportion of seeds that germinate under various conditions (g_{jw}), the success rate of germinated seeds becoming protocorms (q_{jw}) and the rate at which protocorms survive and emerge as above-ground plants (f_{jw}) are based on in situ germination trial data collected in 1995 and 1996. A total of 0.01 mg of orchid seed collected in the fall of 1995 was placed in each seed packet constructed with plankton netting (Rasmussen and Whigham, 1993). The seed packets were then buried under the soil surface in experimental plots on the Shenyenne National Grassland. Number of germinated and imbibed seeds and number of protocorms and seedlings were counted in a total of 48 seed packets collected from the experimental plots in 1996.

The proportion of seeds that do not germinate but remain viable (v_{jw}) is based on an assessment of the number of viable seeds in 20, 0.01 mg seed samples collected in 1995. We do not have any data on seed viability in the soil, but our assumption is that seed viability would remain higher in dry soils. Rasmussen (1995) indicated that the water-repellent testa in orchid seeds will tend to

Table 1
Parameter values for demonstration model

	Contour								
	Deep			Moderate			Shallow		
	Wet	Mid	Dry	Wet	Mid	Dry	Wet	Mid	Dry
v_{jw}	0.5	0.6	0.7	0.5	0.6	0.7	0.5	0.6	0.7
g_{jw}	0.01	0.11	0.05	0.11	0.07	0.01	0.11	0.01	0
r_{jw}	0	5902	4864	9923	2529	0	6615	0	0
q_{jw}	0	0.13	0.06	0.13	0.05	0	0.01	0	0
f_{jw}	0	0.09	0.08	0.09	0.07	0.01	0.09	0	0
z_{jw}	0	0.5	0.25	0.23	0.78	0	0.23	0.09	0
c_{jw}	0	5.46	0.2	5.46	0.2	0	1.0	0.54	0
a_{jw}	0	109	4	109	4	2	20	11	0

keep seeds dry in the soil for considerable periods of time, perhaps enabling them to resist microbial attack that leads to testa decay. The number of seeds produced per above-ground plant was based on estimates of the number of viable capsules produced per flowering plant on 18 transects on the Shenyenne National Grassland between 1994 and 1997, the average number of viable seeds per capsule (see above) and the proportions of flowering plants that occurred under various climate scenarios (Sieg and King, 1995). Survival rates of above-ground plants from one year to the next (z_{jw}) are based on demographic data collected between 1990 and 1994 (Sieg and King, 1995). Plant carrying capacities (c_{jw}) are estimated from monitoring data we have collected on the total number of orchids in each of three pastures over

8 years on the Shenyenne National Grassland. We estimated protocorm carrying capacity (a_{jw}) to be 20 times the carrying capacity of above-ground plants.

The dimensions of the case example create a linear program with approximately 8000 constraints and 8200 variables. The model was built with the high-level programming language 'GAMS' and was solved with the 'C-WHIZ' solver.

4. Results and discussion

4.1. Initial seed dispersal assumptions

Protecting habitat for the orchid is likely to be difficult, with limited resources available. The typ-

Table 2

Expected values of orchid populations from model solutions with the initial seed dispersal assumptions

Year	Base solution	Even allocation	Even allocation for contours 1 and 2
1	2.37	2.37	2.37
2	2.02	1.06	1.85
3	6.79	3.65	5.38
4	9.04	6.75	8.31
5	8.08	6.52	7.59
6	10.75	7.34	9.37
7	15.10	10.64	13.39
8	17.56	13.06	15.88
9	21.30	15.34	18.93
10	27.74	19.72	24.50
11	34.53	24.36	30.67
12	42.40	28.26	37.51
13	53.43	31.39	47.00
14	67.11	32.03	58.94
15	83.42	32.36	73.08
16	101.30	32.69	87.94
17	104.60	32.94	99.40
18	105.91	33.10	103.18
19	106.30	33.21	103.27
20	106.30	33.29	103.27
21	106.30	33.34	103.27
22	106.30	33.37	103.27
23	106.30	33.39	103.27
24	106.30	33.41	103.27
25	106.30	33.42	103.27
Total	1457.55	567.01	1368.18

Table 3

Expected values of orchid populations from model solutions with the conservative seed dispersal assumptions

Year	Base solution	Even allocation	Even allocations for contours 1 and 2	Altered climate probabilities
1	2.37	2.37	2.37	2.19
2	2.02	1.06	1.85	1.88
3	6.79	3.65	5.38	6.30
4	7.71	4.62	6.40	7.08
5	7.83	4.41	6.55	7.10
6	10.48	6.05	8.75	9.59
7	13.70	8.33	11.52	12.56
8	16.23	9.84	13.69	14.84
9	20.35	12.26	17.13	18.86
10	26.40	14.92	22.21	24.92
11	33.22	16.45	27.95	31.75
12	41.81	18.32	35.14	40.81
13	50.14	21.07	40.03	48.08
14	56.78	24.00	44.65	54.35
15	61.47	27.43	48.51	62.18
16	67.61	29.86	53.65	69.92
17	75.04	30.90	59.56	79.53
18	83.16	31.43	66.51	91.07
19	92.99	31.83	75.31	99.15
20	101.54	32.17	85.90	99.31
21	104.11	32.41	93.63	99.46
22	104.98	32.60	96.48	99.50
23	105.34	32.72	98.91	99.51
24	105.66	32.79	100.06	99.52
25	105.81	32.84	100.62	99.53
<i>Total</i>	1303.54	494.30	1122.76	1278.99

ical problem situation, therefore, is to optimally locate a limited amount of habitat over time. Fig. 2 presents the management strategy solved for by the model with the initial seed dispersal assumptions and 50 ha of habitat allowed to be protected (see also, Table 2, Column 1). This solution and the ones to follow strongly suggest that much higher priority should be given to the two lower contours for habitat protection. It is largely within those two contours that the spatial and temporal allocation takes place. The management strategy indicated by the model in this solution has three distinct phases. Initially, habitat is protected around swale complex 2, to assist the fledgling population in establishing itself. Habitat protection gradually increases elsewhere until, by year 16 (depicted in Fig. 2a), a nearly even level of habitat protection is placed in all contour 1 and 2 areas (except around swale complex 2, which is still fully pro-

tected). Then, the solution begins concentrating on the contour 2 areas until, by year 20 (depicted in Fig. 2b), the solution reaches its maximum population, almost completely concentrating on the contour 2 areas. We also mapped the orchid population response to this habitat protection strategy and, not surprisingly, the population closely follows the pattern of protected habitat. The first phase of this strategy is clearly dependent on the initial conditions. The second phase appears to include the lowest contour with the middle contour so as to build a seed bank (it is only in the lowest contour that seeds are produced in the dry climate condition, see Table 1). Once a seed bank is established, the solution focuses on the middle contour areas, implicitly relying on the seed bank during dry years. The sensitivity of this strategy to the climate probabilities used and the importance of applying such a strategy in an adaptive management context will be discussed below.

The spatial and temporal layout of protected habitat, especially with regard to the two lower contours, is indicated to be important. Table 2 also presents solution population results with two limits on spatial/temporal flexibility. The second column in Table 2 shows a solution where the proportion of each swale-contour area protected as habitat is constrained to be the same. This solution represents a simple-minded spatial allocation that simply treats all areas the same (proportionately). This solution indicates a very large loss in orchid population relative to the one in Table 2: from 1458 to 567 plants over 25 years. Most of this loss can be attributed, however, to the allocation to the highest contour, at the expense of the lower two. If it was known that the lower two contours should be given priority, the solution in the third column of Table 2 might be a spatially neutral approach. Here, all 50 ha of habitat are allocated to the lower two contours, but each swale-contour area within those two contours is allocated an equal proportion of habitat. With this approach, the loss in orchid population is much smaller: about 89 plants over 25 years. Most of this loss is observed in time periods 11–16, with a 12.5% reduction. The maximum population level in the third column in Table 2 is only about 3% lower than the maximum reached in column 1. Thus, the spatial placement of habitat in the lower two contours is indicated to be more important for the middle years of a recovery period than for the maximum that is eventually reached. We will investigate the robustness of this conclusion further.

4.2. *Conservative seed dispersal assumptions*

Fig. 3 and column 1 of Table 3 present the optimized solution for the model with the more conservative seed dispersal assumptions and, again, 50 ha of protected habitat is allowed. Priority is still indicated to be much higher for the lower two contour areas than for the highest contour area. Also note that the approach to the maximum population level is considerably slower (as expected) with these conservative seed disper-

sal assumptions. The basic strategy suggested by this solution is, however, quite similar to the one in Fig. 2. The initial phase again protects orchid habitat around the initial population. By year 20 (depicted in Fig. 3a), a substantial amount of habitat in all contour 1 and 2 areas is protected, but, the spatial effect of the initial conditions obviously remains much longer than in Fig. 2a, due to the slower and more difficult expansion of the orchid implied by the conservative seed dispersal assumptions. By year 25, the solution has still not reached a maximum population level (column 1, Table 3) and further expanding the time horizon created a model that we were not able to solve with available hardware and software. The allocation in Fig. 3b, however, is quite similar to Fig. 2b. As before, the orchid population associated with this solution closely follows the pattern of habitat protection.

In column 2, Table 3, we present a solution similar to column 2 of Table 2, where the proportion of each swale-contour area protected as habitat is constrained to be the same. Results are similar to those in Table 2, with a very large loss in orchid population. This is, again, largely attributable to the allocation of habitat to the contour 3 areas at the expense of the contour 1 and 2 areas.

In column 3 of Table 3, a solution similar to column 3 in Table 2 is presented, where all 50 ha are allocated to the lower two contours, but with an equal proportion protected in each swale-contour area within those two contours. The loss in orchid population is about 19.5% for years 13–20. The basic pattern is quite similar to that in Table 2, but the more conservative dispersal assumptions appear to make the spatial allocation in the middle years of recovery a bit more important than before. The robustness of this basic solution strategy to significantly different seed dispersal assumptions is noteworthy, but we found that the third phase of this strategy was highly sensitive to the climate condition probabilities.

Recall that in the ground water height data from the second well that we were able to obtain, the year 1984 was not indicated to be a 'wet' year

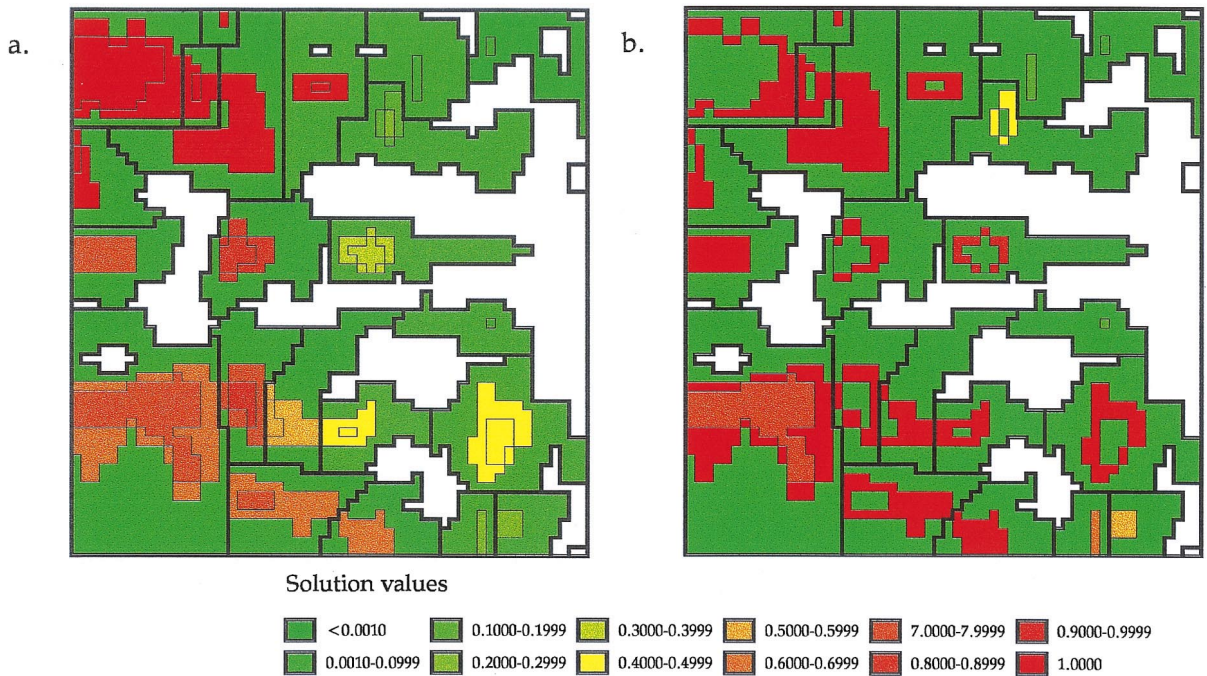


Fig. 3

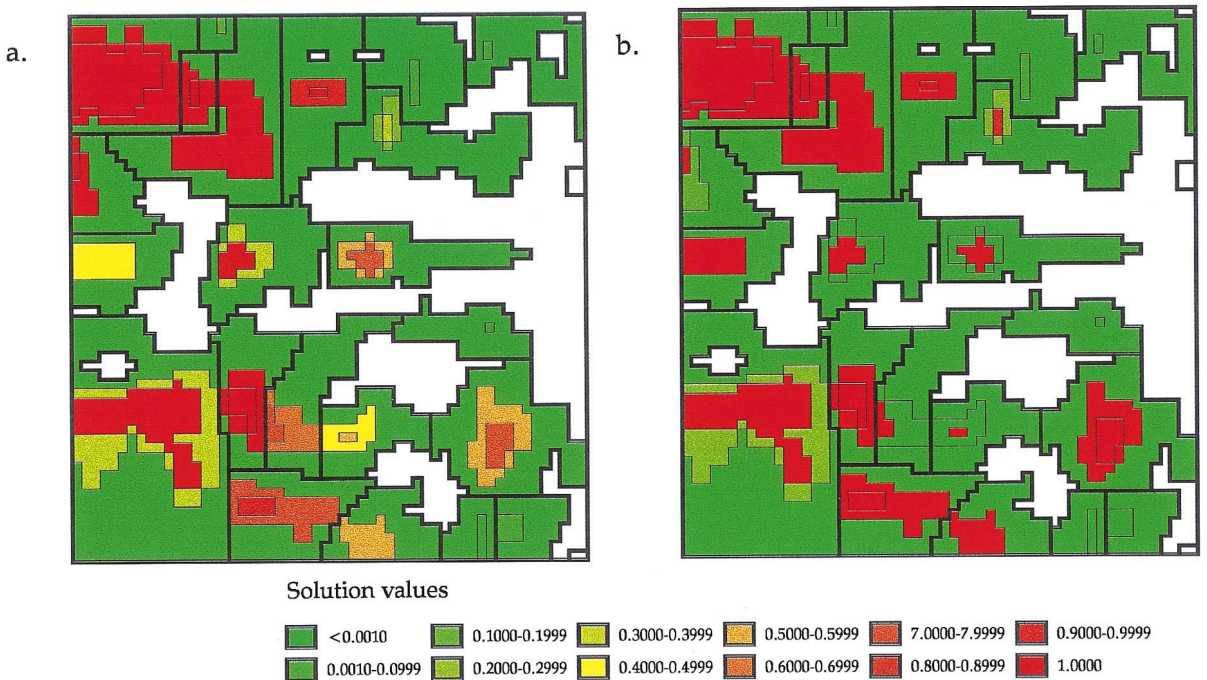


Fig. 4

Fig. 3. Area allocated to orchid habitat (white areas are non-habitat) in base solution with conservative seed dispersal assumptions in time period 20 (a) and in time period 25 (b).

Fig. 4. Area allocated to orchid habitat (white areas are non-habitat) in solution with altered climate probabilities and with conservative seed dispersal assumptions in time period 20 (a) and in time period 25 (b).

as it was in the first well's data. Making this single adjustment to the estimates of climate condition would reverse the probabilities of the middle and wet climate conditions (now 0.381 for climate condition 2 and 0.333 for climate condition 3). Fig. 4 and column 4 of Table 3 depict the solution of the model that results from making this adjustment with the conservative seed dispersal assumptions (the initial model responded quite similarly to this change in climate condition probabilities). The first two phases of the solution strategy with these altered probabilities are similar to those just discussed, as evidenced by the similarity in Fig. 3a and Fig. 4a (year 20 in both cases). By year 25, however, the third phase strategy in Fig. 4b (see also column 4, Table 3) is quite different. Now, the lowest contour areas are completely protected, with ancillary middle contour areas included as possible given the 50 ha total limit. The altered probabilities are a bit 'drier', based on one less historical year being considered in condition 3 (and thus one more in condition 2). With these slightly drier probabilities, it is now preferable to focus on the lowest contours that provide habitat in the driest years, even after a large seed bank is established.

5. Conclusion

The sensitivity to the climate probabilities points out the importance of using a model such as ours (where risk is handled with fixed probabilities and optimization is based on expected values) in an adaptive management process as new data become available (Walters, 1986). Clearly, the tenability of such a model erodes rapidly with time as variances around expected values increase. These weaknesses would be ameliorated if the status of the system being modeled was monitored regularly and the model was re-run with new initial conditions as they became known. In such a process, if circumstances never allowed the orchid to recover very far (because, for example, of a string of dry years) the latter two phases of the management strategies described above might never be implemented. If

events proceed close to the expected value predictions, then the calculated strategy might remain tenable much longer. Conversely, if the third phase was reached, but became untenable because of a random or catastrophic event, the adaptive process would 're-set' the management strategy to an initial phase based on the new conditions. No clear-cut strategy to managing risk is ever available, but the analysis above suggests that arbitrary timing and placement of orchid habitat protection will not be as effective as a more calculated approach.

The most important structural assumption in our model is the long-term viability of seeds, making the orchid resistant to catastrophic loss. If possible, research efforts should test this assumption. If evidence that the orchid is vulnerable to catastrophic loss did surface, then approaches that are more risk-averse than our model might be of more interest. More information on the orchid's population dynamics, including seed dispersal and germination ecology, could also be quite useful. This study is clearly an exploratory effort and should be viewed accordingly. Additional research is indicated for capturing the population dynamics of the western prairie fringed orchid in mathematical models, including optimization formulations as we have studied here.

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