Assisted Migration as a Conservation Strategy for Rapid Climate Change: Investigating Extended Photoperiod and Mycobiont Distributions for *Habenaria repens* Nuttall (Orchidaceae) as a Case Study

By

Brian George Keel

A dissertation in partial fulfillment of the requirements for the degree of

Doctor of Philosophy (Environmental Studies)

at

Antioch University New England

2007

"ASSISTED MIGRATION" chapter 3

Abstract

This dissertation proposes assisted migration (the intentional movement of a plant beyond the boundary of its present range) as a plant conservation strategy in a changing climate and within a fragmented landscape. Orchids are a unique family of plants that have an obligate requirement for mycorrhizal fungi, and therefore, an ideal group to use as a model for plant/microbe conservation in a changing climate. I examined two factors that may influence the application of assisted migration to orchids. I evaluated the effects of an extended photoperiod on orchid seed germination and seedling development (plants migrating to higher latitudes will be subjected to extended photoperiods during the growing season relative to the seed source), and I assessed the range of a specific terrestrial orchid's mycobionts. Habenaria repens Nuttall, a native of the New World tropics and subtropics, was used as a model for North American terrestrial orchids. Habenaria repens seed from Florida was subjected to the photoperiod of three locations, 14.75 h (seed source), 16.25 h (southern Pennsylvania), and 20 h (northern Quebec). Percent seed germination was highest for the 16.25 h photoperiod (37.0%), and lowest for the 20 h photoperiod (15.1%). After germination, seedlings showed a trend for better growth as the photoperiod was extended with best growth attained under the 20 h photoperiod. To determine the range of *H. repens*' mycobionts, nylon mesh seed packets that permit fungi to enter and form mycorrhizal associations with the seed were employed as a means of capturing fungi. Seed packets were sown at five sites within the Atlantic coastal plain in North Carolina, Virginia and Maryland, and one site in upstate New York. Retrieved seed packets produced six fungal strains, all tentatively identified as members of the genus *Epulorhiza*. Findings of this project emphasize that the successful establishment of an orchid population at a particular site, assuming the site is otherwise acceptable for the orchid, is ultimately dependent on the presence of compatible mycobiont strains.

Table of Contents

Acknowledgements		i
Abstract		ii
Introduction		1
Chapter 1	Plants and Climate Change	6
Chapter 2	Orchids, Mycobionts and Climate Change	43
Chapter 3	Assisted Migration: A Strategy for Plant Conservation in a Changing Climate	65
Chapter 4	The Influence of Extended Photoperiod on Seed Germination, Seedling Development and Growth of the Terrestrial Orchid <i>Habenaria repens</i>	86
Chapter 5	Mycobionts of Habenaria repens in the Northern Part of its Range	107
Chapter 6	Orchids, Mycobionts, Climate Change and Long-Term Conservation	146
Literature Cited		160

Chapter 3

Assisted Migration: A Strategy for Plant Conservation in a Changing Climate

Introduction

The present climate change, which will most likely take place over the next 50 to 100 years (Pastor & Post 1988, Davis 1989, Martin 1996, Kullman 2002), is expected to be a general warming of the global climate. A temperature increase of only 2° C may cause responses among plant species (Davis 1989). One of the predicted vegetation responses to climate change is the movement of plants to higher latitudes and altitudes as the climate to which they are adapted is displaced (Jump & Penuelas 2005). Evidence of plant movements related to the present climate change are being reported (Sturm et al. 2001, Kullman 2002, Walther et al. 2002, Parmesan & Yohe 2003, Penuelas & Boada 2003, Walther 2004). These movements, in a world without the intense or pervasive influence of humans may allow most plants to endure the changing climate. However, the rapidly increasing global human population and the anthropogenic effects now evident in every ecosystem (Ashley et al. 2003) along with attendant resource demands and landscape scale alterations is putting may species at risk of extinction. The scale of the expected extinctions is so great that scientists have called it a biodiversity crisis (McKinny 1998, Pavlik 1996, Pullin 2002). This biodiversity crisis has prompted several authors to make suggestions for long-term species survival. Some authors stress that the primary aim in conservation should be to preserve as much habitat as possible (Thomas 1994, Hanski 1998). The conservation of imperiled habitat types with high endemism is also important for the conservation of regional biodiversity (Gitlin et al. 2006). Thrall et al. (2000) stated that colonization processes must be preserved through the maintenance of existing populations, and the setting aside of habitats where species are not currently present. These are good strategies for dealing with the present biodiversity crisis. However, a changing global climate, I believe, will require a strategy that allows conservation biologists to be proactive.

The process of plant migration driven by climate change is becoming of great importance for plant conservation. Natural migration in a changing climate is the movement of species to locations where they did not historically exist. This movement is a strategy employed by plants to track shifting habitats, but the current human-induced landscape scale changes limit the ability of plants to migrate and adapt to changing climatic conditions. However, in a fragmented landscape, along with habitat destruction as well as alien species invasions, many species will lose their ability to shift their geographic range (Beissinger & McCullough 2002, Etterson 2004) and if not able to migrate to new suitable habitats some species could go locally extinct (Primack & Miao 1992). Habitat destruction is commonly deemed the greatest threat to biodiversity(Cameron et al. 2004), but this may no longer be the case if climate change continues unabated, for the combination of habitat destruction and climate change will be particularly destructive (Cameron et al. 2004).

Some plants will have difficulty migrating quickly enough to track climate change (Neilson et al. 2005), or will be outright prevented from migration and might perish attempting to move through a fragmented landscape that human activity has rendered increasingly impassible (Pitelka 1997, Etterson & Shaw 2001, Davis & Shaw 2001, Jump & Penuelas 2005). Human land use may also present an impediment to gene flow among

plant populations (Davis & Shaw 2001). Even in landscapes that have not been directly altered, rapid climate change may pose an extinction threat; plants unable to emigrate upward in tropical cloud forests, for instance, may be at risk from the rising cloud base which is caused by rising sea and land surface temperatures (Nadkarni & Solano 2002).

In these situations where plants are prevented from migration, human intervention will be necessary to prevent extinction. I call this intervention "assisted migration", which is the employment of techniques to ensure the maintenance of plant populations in a changing global environment through the intentional creation of populations beyond the boundary of a plant's present range. Barlow (2000) reinforced this form of intervention when she made the statement that as temperatures increase and rainfall patterns shift with a changing climate, helping plants track climate change by moving them from one forest patch to another will become a routine tactic. Based on predictions of climate change effects on plants, this would require, in most cases, movement of plants north or upslope for the tracking of suitable habitats. In the case of areas such as western North America with steep environmental gradients and topographic complexity, range shifts could be in any direction (Shafer et al. 2001). Before introducing the concept of assisted migration, it is necessary to understand just how far and how fast plants will need to migrate.

Tracking Rapid Climate Change

Computer models have been devised to help understand the changes in climate and vegetation that will come about as a consequence of greenhouse gas accumulation in the atmosphere and can help determine approximate required migration distances. Hansen et al. (2001) summarized the results of seven general circulation models (GCM) developed

to predict changes in climate. A base-line doubling of atmospheric CO₂ was used for the models. These models show mean annual temperature increases for the coterminous United States to vary from 3.3° C to 5.8° C with the greatest warming to be experienced at higher latitudes. These predictions aside, the air temperature over most of the United States and Canada has increased 0-2°C during the past century (Hansen et al. 2001). Since the use of fossil fuels and the burning of forests continue world wide, it is a safe assumption that the air temperature of North America and the world will continue to rise. Using a maximum of 5.8° C (average worse-case scenario) predicted temperature increase from the models summarized by Hansen et al. (2001), plants would need to expand their northern range boundaries (i.e., migrate) approximately 580 km, based on Davis' (1989) predicted movement of 100 km for each degree C of warming. As an example, Habenaria repens, an orchid whose present northern range boundary is in east central North Carolina would need to expand its northern range 580 km into southern Pennsylvania. Researchers in Europe estimate even greater required migration distances than 580 km by the time the climate stabilizes. One estimate is that with a temperature increase of 5^0 C the major vegetation zones in Europe will shift northward by about 1100 km (Drake 2000). A need to migrate approximately 580 km in 100 years would require a migration rate of 5.80 km per year, a rate that may not be possible for some plants without human assistance.

Tree species are capable of relatively rapid migration when compared to herbaceous plants, but trees may not be able to migrate fast enough to track future climate change. The fossil record shows common migration rates for trees of 20 to 40 km per century with a few exceptional examples of 100 to 150 km migrations per century, far

below the current projections for the 21st century of 300 to 500 km per century (Davis & Shaw 2001). This chapter will focus on herbaceous plants; as will be seen, herbaceous plants will be at great risk where rapid migration is necessary.

Migration in the Mountains

Migration caused by climate change refers not only to latitudinal migration, but also to altitudinal migration, and rapid movement of montane communities to track shifting montane zones (Hannah 2002) will be necessary for plants to track climatic change. When comparing climate gradients between latitude and altitude, 200 m of elevation equals approximately 1^o of latitude (Gaston 2003); 1^o of latitude is equal to approximately 114 km. Temperature increases much more rapidly with elevation in mountainous terrain, about 1^o C per 160 m, than with latitude, about 1^o C per 150 km, at higher latitudes (McCarty 2001), and about 1^o C per 1000 km north and south of the equator (Madigosky 2004). Climate gradients and microclimate variability associated with elevation and topography produce a wide range of climatic conditions in montane regions. This wide range of conditions and makes for marked changes in range and abundance in montane areas when compared to non-montane areas (Hannah 2002).

McCarty (2001) in a review of the ecological effect of climate change on plants in the Swiss Alps reported that the rate of upward shift was found to be between 1 - 4 m per decade among 9 plant species studied. Based solely on the change in mean temperature over the last 90 years, these movements are slower than the expected 8 - 10 m per decade needed to keep up with the present climate change. Researchers have speculated that the plants in their study might be unable to respond successfully to a more rapid climate change (McCarty 2001). However, Kullman (2002) studying trees and shrubs in the Swedish Scandes reported predictions of the upward movement of altitudinal range-margins are expected to be on the order of 400 - 600 m over the next 100 years or 40 – 60 m per decade, much faster than the 8 – 10 m per decade required movement suggested by McCarty (2001). Actual range-margin expansions for trees and shrubs as found by Kullman (2002) varied considerably between species. Range-margin expansions of four tree and shrub species over the past 50 years varied from 375 m for *Sorbus aucuparia* L. and 340 m for *Pinus sylvestris* L. to 120 m for *Salix glauca* L. and *Salix phylicifolia* L., a variation of range-margin expansions between 24 and 75 m per decade (Kullman 2002). While McCarty's (2001) review covered herbaceous plants known to have slow dispersal rates, Kullman (2002) worked with trees and shrubs; trees are known to be capable of rapid dispersal rates (relative to herbs). This might account for the differences in the reported migration rates.

Other mountainous parts of Europe are experiencing plant movements. In the Montseny Mountains of Catalonia, northeast Spain, upward shifts in Mediterranean vegetation have already taken place caused by a $1.2 - 1.4^{\circ}$ C increase in annual temperature. The beech forests have migrated upwards about 70 m in the last 55 years at the higher elevations of 1600 - 1700 m (the actual pre and post migration altitudes were not given). On mountains of lesser stature at medium elevations of 1000 – 1400, m *Fagus sylvatica* (beech) forests have migrated upwards to mountain summits and have replaced *Calluna vulgaris* (heather) heathlands and grasslands (Penuelas & Boada 2003). Fortunately heathlands and grasslands are common in the Montseny Mountains or these

ecosystems would be at risk of extinction. Unlike the heathlands and grasslands in the Montseny Mountains, some montane plants in Scotland may very well go extinct.

Plant conservationists in the Scottish Highlands believe that climate change has the potential to cause the extinction of rare arctic-alpine plants in much of the Highlands. These arctic-alpine plants are already at or near the top of the mountains and there is nowhere for the plants to go. They grow under distinct conditions defined by calcareous soils and severe climate, and there are few mountains with this combination of conditions. Unless the plants can jump to another mountain, a distinctly remote possibility without human intervention, there is little chance of survival (Mackinley & Mardon 2005).

More information on shifting montane habitats comes from the cloud forests of Costa Rica, and from the Hawaiian island of Maui. Recent evidence shows that the cloud base of the cloud forests of Costa Rica is rising (Nadkarni & Solano 2002), and Seaton (2004, per. comm.) raised the question whether orchids, or other cloud forest dependent plants, will be able to migrate quickly enough up mountainsides to avoid desiccation. From their research on Maui, Loope and Giambelluca (1998) concluded that temperature tolerance zones for both native and introduced species may shift upward by roughly 360 – 450 m with a change in ocean temperatures and an increase in mean air temperature at sea level of $2 - 2.5^{\circ}$ C.

Availability of suitable substrate and acceptable physical conditions are not the only challenges to the colonization of new sites for some plants. Besides the difficulty of keeping up with a rapidly changing climate, which some plants may have the ability to do, many plants must also contend with a fragmented landscape through which they will need to navigate.

Landscape Fragmentation and Habitat Destruction: Compounding the Risk of Extinction

The risk of extinction is increased for plants growing in highly fragmented landscapes such as the eastern seaboard of the United States or Western Europe. These areas of the world are also experiencing habitat destruction, a situation that greatly decreases the ability of a plant to cope with climate change. Landscape fragmentation isolates populations and poses problems for species fitness and population viability, and may also threaten species in other ways depending upon the plants' specific biological characteristics (Kolb & Diekmann 2005).

If habitat patches are not sufficiently well-connected, gene flow by pollen and propagule dispersal will be prevented, increasing genetic isolation of populations. Reduction in gene flow threatens populations through genetic factors such as an increase in genetic drift and inbreeding depression (Jump & Penuelas 2005). These genetic problems combined with demographic factors such as changes in pollinator behavior and altered mating systems, caused by habitat fragmentation, can result in an increased risk of population extinction (Jump & Penuelas 2005). Demographic stochasticity and the inherently poor dispersal ability of many species can be compounded by habitat fragmentation, and as the distance between habitat patches increases and the surrounding matrix becomes more inhospitable, the probability of population establishment declines rapidly, increasing the risk of extinction (Jump & Penuelas 2005). Even for a good disperser and colonizer, landscape fragmentation and habitat destruction could pose a serious threat if the distance between suitable habitat patches is greater than the dispersal ability of the plant. The combination of landscape fragmentation and habitat destruction is an even greater threat to plants with poor dispersal and/or colonization ability.

Primack and Miao (1992) performed an experiment to test the dispersal ability of annual herbaceous plants. Their results indicate that low dispersal ability can limit the distribution of plant species on a local scale; even those species that produce abundant seed were apparently unable to reach potentially suitable sites located less than 100 m from large natural populations over a 20 year observation period. Rare plant species may be particularly vulnerable to extinction because they generally have few populations to serve as focal points for dispersal and tend to be poor dispersers (Primack & Miao 1992). The risk of extinction also increases as presently occupied sites become untenable because of climate change. In a situation in which only one or a few relict populations of a plant remain, it is erroneous to assume that the populations are surviving at sites with optimum conditions (Ramsay & Stewart 1998). The populations simply may not yet have been lost by destruction of the sites or the sites may not yet have become untenable from changing environmental conditions.

Landscape fragmentation and a decrease in the amount of available habitat caused by habitat destruction, in combination with a changing climate will require plant conservationists to be proactive to prevent extinctions. Destruction of habitat refers to the destruction both of sites where the plant is present and of sites which may become, in the future, suitable habitat in a changing climate. Therefore, habitat preservation in a changing climate is a two-fold problem, involving preservation of the site where a plant is presently growing and preservation of sites where the plant might grow in the future with shifting habitats. In a changing climate if a landscape is fragmented to the point that a particular plant cannot migrate on its own, it may be possible to assist the migration of the plant, provided suitable habitat can be found within the fragmented landscape.

Assisted Migration as a Conservation Strategy

When implementing plant conservation projects in the foreseeable future, conservationists must ask questions such as these: (1) Will the site of the present conservation project remain within the range of the plant throughout the time span of the present climate change? (2) Where within the plant's present range will the conservation project be implemented: the interior of the range, near its periphery, the northern or southern extremity, the upper or lower altitudinal boundary of the range? (3) What effect will a changing environment have on projects being implemented at this point in time; will the present work be for naught because of a changing climate and shifting habitats? Answers to these and similar questions should dictate which conservation strategy is applied.

The four basic strategies of plant conservation currently in use are restorations, reintroductions, introductions and translocations. Restoration is employed when a habitat has been damaged or destroyed. As part of that restoration, plants once indigenous to that habitat are restored to the site. Reintroduction (called reestablishment or restoration by some researchers) is used where the habitat is intact but a plant has been extirpated. An introduction establishes a population at a location within the range of the plant where it historically was not present. For a translocation some or all plants are removed from a site and moved to a new site within the plant's present range.

The World Conservation Union/Species Survival Commission (IUCN/SSC) (1995) guidelines for reintroductions prepared by the SSC Re-introduction Specialist Group list four plant conservation strategies: reintroduction, conservation/benign introductions, reinforcement/supplementation and translocation. The IUCN/SSC (1995) definitions of reintroduction and translocation are the same as defined above. Conservation/benign introductions is a method for establishing a species in an appropriate habitat and eco-geographical area outside its recorded range, a method to be used only when there is no remaining habitat left within the species' historic range (IUCN/SSC 1995). A fourth conservation tool in the IUCN/SSC (1995) guidelines is the reinforcement/supplementation of an existing conspecific population by the addition of individuals. All of these strategies were designed for use in a stable climate and within or just outside the present range of the target plant.

I argue that with rapid climate change and pervasive landscape fragmentation and habitat destruction which both can prevent some plants from migrating, assisted migration is an important conservation strategy. I define assisted migration as

The intentional establishment of populations or metapopulations beyond the boundary of a species' historic range for the purpose of tracking suitable habitats through a period of changing climate. This might involve migration between islands, up mountain slopes, and between mountain tops (Keel 2005).

Assisted migration does not in any way replace other conservation strategies. More than a strategy, assisted migration is a mental paradigm shift from the implementation of conservation projects within a stable but dynamic environment to working within an environment that has begun to change, and taking that changing environment into account during the planning and implementation of conservation projects from now into the foreseeable future. Assisted migration may also include the conservation of areas that are not important for species preservation at present but will become very important as habitats shift in response to climate change. This is not to say we should indiscriminately move plants, because the assisted migration of any plant to a site beyond its present range will constitute the introduction of an alien species. However, the danger of not applying assisted migration and leaving population spread to natural mechanisms may result in the loss of species that might otherwise have survived (McLachlan et al. 2007). Therefore, assisted migration must be performed on a case by case basis as a scientific experiment. Assisted migration proposals should require evidence of imminent threat, a quantitative model of predicted outcome and a management plan (McLachlan et al. 2007). Monitoring will be required for several years after a project is implemented, not only to assess results, but also to mitigate any unforeseen problems that arise from the introduction. Unfortunately there is the possibility of plants being moved by well meaning individuals without forethought of the consequences. It is relatively easy for a private citizen to legally move species and this could pose a problem because historically there has been little accountability for unwanted invasive species, and most natural resource agencies lack policies to address this issue (McLachlan et al. 2007). This situation will require rectification in the form of public agency policies as assisted migration moves to the forefront of conservation issues in a changing climate. However, the magnitude of the impending climate-driven extinctions requires immediate action and delays in policy formulation and implementation will make the situation even more urgent (McLachlan et al. 2007).

Regardless of public policy, assisted migration can be applied in such a way as to minimize the problem of invasive species.

Assisted migration should move a plant just fast enough to track shifting habitats and is not intended for long-distance introductions; effort may be wasted attempting a long-distance introduction into climatically inhospitable areas where a plant can not survive. If climate is a constraining factor of range limits or distribution within that range, then moving a plant just fast enough to track a changing climate will help keep the species under climatic restraint and help mitigate the alien species problem. At least some of the species that fall into the risk categories listed in Table 3.1 would not be aggressive colonizers or prolific reproducers (i.e., inherently invasive species most likely would not be at risk), and are not likely to become problem invasive species as a consequence of assisted migration. Once a species is determined a candidate for assisted migration, site selection for the introduction will require critical investigation because the introduction of an alien species to a new location will cause a change in species composition. However, if the extinction of a species is prevented, there is more to be gained than lost by the introduction, provided species are not extirpated from the plant community at the introduction site.

Plant communities are naturally dynamic with species composition changing spatially and temporally, and plant communities will be disrupted by climate change (Ritchie 1986). Hunter (1999) took the dynamics of community continuity one step further when he stated that modern plant communities are the products of current biotic and environmental conditions. These communities often contain combinations of species that did not occur in the past and are unlikely to occur in the future as species respond individually to climate change (Davis 1983a, Kullman 2002).

Under a changing climate, species ranges are not static. Species are sensitive and respond to minor changes in climate with subsequent expansions and contractions of ranges (Davis 1983a). These range variations can reflect differences in climate forcing, climate response and dispersal behavior (Johnstone & Chapin 2003). Plant species will respond individualistically with rates of migration varying spatially and temporally, and with different time lags, resulting in plant communities that will be disrupted for many decades (Davis 1989, Johnstone & Chapin 2003). Variation in both the rate of climate change and the rate at which individual plants migrate will be a major determinant of community composition in the future.

During the Pleistocene, in areas with high rates of climate change such as at high latitudes, initial colonization was probably by fast-migrating species, and in areas with low rates of climate change less mobile species were found (Neilson et al. 2005). During the present rapid climate change Neilson et al. (2005) believe plants will be sorted into bands along a migrational front, with fast moving (most invasive) dispersers being trailed by slower (less invasive) dispersers. The slower moving species may perhaps be at the most risk of local extinction. The rapidly migrating native plants will increasingly invade communities containing more sedentary, endemic or late-successional species and enhance the risk of local or total extinction of some species (Neilson et al. 2005). Other factors will also influence the colonization of plants at sites where they previously did not grow.

Perry et al. (1990) described the mix of species during migration and colonization by stating that migrating plants move within a milieu of interactions with other plants of both the same and different species, and the success of plants on any given site is probably determined by the plant species already there, whether they are recently established newcomers or long-time residents. It is hypothesized that plant species immigration will be facilitated (at least from a soils organism standpoint) if the immigrant and at least a few of the residents of the site being colonized occur together elsewhere (Perry et al. 1990).

I have attempted to demonstrate in the above discussion that the desire to keep present communities intact, which will be difficult if not impossible in a changing climate, should not be a deterrent for consideration of assisted migration as a conservation strategy. The primary consideration must be the prevention of species extinctions.

Risk Assessment for Assisted Migration

A plant would not be at risk of extinction during climate change if the ratio of population extinctions to population colonizations remained relatively constant. Also, there would be little risk of extinction if a contraction of the southern or down slope boundary of its range caused by population extinctions was matched by net colonizations beyond the northern or up slope boundary, constituting a shift in the range of the species. Although anthropogenic climate change is not a natural phenomenon, plant response to that change is natural (natural = non-human caused phenomenon) (Luken & Thieret 1997), and it will be difficult to determine which responses to climate change are driven

by natural versus human phenomena. Regardless of the cause of climate change leading to plant responses, it is important to determine extinction risk due to an inability to migrate, or migrate quickly enough, latitudinally or up slope in response to climate change. Orchids and monotropes which require mycorrhizal fungi for seed germination, seedling development and, for some species, growth throughout their life stages, have the additional problem of locating a compatible mycobiont (Rasmussen 2002) during migration. The pollination vector (wind or animal) and the proximity of plant populations will also influence the ability of a plant to migrate.

A major problem for risk assessment in a changing climate will be to separate the effects of climate change from the background noise of other environmental threats. However, there are some indicators, detectable at a regional or local scale, that can be used to help determine if the climate has changed enough locally to warrant consideration of assisted migration. Some of the clues are changes in plant communities, a shift in isotherms, and shifts in plant phenological events such as earlier flowering or leaf-out. An important clue is if populations in the southern or lower elevation portions of some plant ranges are decreasing and at the same time populations at the northern or upper elevation limit of the ranges are stable or shifting.

Climate change working synergistically within the framework of landscape fragmentation, habitat destruction, species invasion and other environmental problems will threaten species with extinction. I have identified several risk factors that will help conservationists key in on prime candidates for assisted migration. These factors, if taken by themselves for most plant species at risk of local or total extinction, could be addressed through the basic strategies of plant conservation that are currently in use as mentioned above. It is the addition of a changing climate that may require the application of assisted migration.

Table 3.1 Risk Factors for Assessing the Need for Assisted Migration

An endemic species with a limited range

An endangered species

A species that is not an effective disperser

A species that requires a unique habitat

A species with narrow environmental tolerances

Compressed latitudinal or altitudinal range

Species with only one or a few populations

Small population size

Less competitive than invasive species or other native species

Candidates for Assisted Migration

Here I present several examples of plants that may be candidates for assisted migration, and those risk factors assignable to these plants. The first is the orchid *Platanthera pallida* P. M. Brown that may be in greater danger of extinction from urban sprawl and isolation than directly from climate change, and without assisted migration through a highly fragmented landscape may have little chance of survival. It is a rare endemic that is restricted to three sites in eastern Long Island, New York, where it grows in dry interdunal hollows among pitch pine and scrub oak (Brown 1997). *Platanthera pallida* requires a unique habitat, has a compressed latitudinal range, and is a species with only a few populations.

The second example is another orchid growing in an area of high human use. *Triphora craigheadii* Luer is an endangered endemic restricted to a few sites in three west central Florida counties (Brown 2002). *Triphora craigheadii* grows in rich, deciduous and mixed damp woodlands and is an endemic species with a compressed latitudinal range.

The third orchid is the endangered *Ponthieva brittoniae* Ames, known only from Dade County, Florida, the Bahamas and Cuba. *Ponthieva brittoniae* has not been seen in the wilds of Florida for many years (Brown 2002), and may have been extirpated from the United States. *Ponthieva brittoniae* would require reintroduction into southern Florida, and then assistance migration could be applied to move it up the Florida peninsula to track shifting habitats. Orchids and other herbaceous plants are certainly not the only plants that may require assisted migration for long-term survival.

The highly endangered conifer *Torreya taxifolia* Arn. is endemic to bluffs and ravines along a 35 km stretch on the east side of the Apalachicola River in the panhandle of Florida (Schwartz et al. 2000). It is believed by some that the present range of *T. taxifolia* in northern Florida should be viewed not as its native range but rather as the tree's range at the peak of the last glaciation, and it is believed that in the distant past, *T. taxifolia* was a member of the Appalachian forest community (Barlow & Martin 2004). The hypothesized reasons for *T. taxifolia* being left behind as the glacier retreated was the increase in the use of fire by humans, which acted as a deterrent to the migration of fire-intolerant *T. taxifolia*, along with the extirpation of squirrels and tortoises, used by humans as food, that are believed to have been the dispersers of its large fleshy seeds (Barlow & Martin 2004). At this writing an attempt is underway for a long distance

introduction of *T. taxifolia* to sites in the southern Appalachian Mountains (Barlow & Martin 2004). This introduction attempt is an assisted migration but differs from present assisted migration projects that might be initiated under the present climate change. *Torreya taxifolia* will be moved to track the last great climate warming that took place in the Pleistocene Epoch and continued into the present Holocene Epoch. Once established in the southern Appalachian Mountains, *T. taxifolia* may then require assisted migration (other track shifting habitats during the present climate change. Assisted migration (other than for exceptions such as *T. taxifolia*), as I present the concept and will reemphasize here, is designed to migrate a plant only fast enough to track shifting habitats, and a series of moves will be required to keep the plant within its shifting natural range and in pace with a changing climate.

Tracking Temperature Change

Moving a plant to track shifting habitats will need to be as gradual or as rapid as the climate is changing. Therefore, a method is needed to track climate change to determine how far and how fast to migrate the plant. Woodward (1987) indicated that the major constraint to the northward migration of a plant is the minimum temperature the plant can endure. If temperature is the principal restraining factor, the northern range boundary of the plant should fall roughly along an isotherm (an isotherm is a line on a map joining points of equal mean temperature), and the temperature of the isotherm should be the minimum temperature the plant can withstand. As the climate warms and isotherms shift northward, movement of an isotherm can be tracked by examining weather data. At least two investigations have noted upward altitudinal shifts in isotherms (Beniston et al. 1997, Penuelas & Boada 2003). Beniston et al. (1997) mention that an upward shift of approximately 100 m in the level of the 0^0 C isotherm took place in the mid 1970s. This isotherm change was detected from data averaged from 10 stations in South America and coincided with an increase in tropical sea surface temperatures. Penuelas & Boada (2003) reported an increase of about 1.2 - 1.4 ^oC in the Montseny mountains of NE Spain which resulted in an upward shift in temperature isotherms of 240-280 m. By following the movement of a minimum temperature isotherm, it may be possible to track the northward or upward expansion of a plant's range over time. Until the climate stabilizes, which is predicted to occur over the next 50 to 100 years (Pastor & Post 1988, Davis 1989, Martin 1996, Kullman 2002), it will be necessary to periodically track shifting isotherms and continue migration of a plant. Once it is determined that the range of the plant has expanded, and risk assessment warrants assisted migration, consideration can be given to the technical aspects of establishing a new population.

Conclusions

In a rapidly changing climate, human intervention in the form of assisted migration may be necessary to prevent the extinction of select plant species by the establishment of new populations beyond a plant's range in locations where historically the plant never grew. However, for plant conservationists with no prior experience of working in a rapidly changing climate, it will be difficult to ascertain if the decline of a plant population is from changing climatic conditions or from other causes. If it is decided that assisted migration is necessary, new sites will need to be located that contain climatic and other abiotic and biotic conditions conducive to survival of the plant. If it is not possible to determine the cause of a population decline, then in the interim until our knowledge of climate change and plant migration develops, it may be necessary to employ a variety of techniques to keep plants from going extinct, including the collection and storage of seed in a seed bank and/or the propagation of plants in botanical gardens.

The goal of any plant conservation project should be the creation of populations or meta-populations that are able to exist without human assistance for the foreseeable future. For those plants obligate to mycorrhizal fungi, this goal will also require the conservation of fungal symbionts and an understanding of fungal ranges and migration. For orchids and other plants with an obligate need for mycorrhizal fungi, before new populations can be established it will be necessary to determine if the appropriate species of fungi are present in the soil, or if they can or should be introduced (i.e., assisted to migrate along with the plant). There have been few or no studies of the intentional movement of fungi in a changing climate, and whether or not assisted migration would be necessary or is possible for fungi. There are risks associated with the intentional movement of fungi that are not present with the intentional movement of plants; Chapter 6 will examine those risks. Photoperiod is another factor that might influence the assisted migration of an orchid. The next chapter will explore the possibility of photoperiod as either a constraint or a stimulus to the assisted migration of orchids. Literature Cited

- Ashley, M. V., M. F. Willson, O. R. W. Pergams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionarily enlightened management. Biological Conservation 111:115-123.
- Barlow, C. 2000. The ghosts of evolution. Basic Books, New York, N. Y.
- Barlow, C., and P. S. Martin. 2004. Assisted migration for an endangered tree. Wild Earth Fall/Winter 2004-2005.
- Beissinger, S. R., and D. R. McCullough, editors 2002. Population viability analysis. The University of Chicago Press, Chicago, Il.
- Beniston, M., H. F. Diaz, and R. S. Bradley. 1997. Climate change at high elevation sites: an overview. Climatic Change 36:233-251.
- Brown, P. M. 1997. Wild orchids of the northeastern United States. Cornell University Press, Ithaca, N. Y.
- Brown, P. M. 2002. Wild orchids of Florida: with reference to the Atlantic and Gulf Coastal Plains. Uni. of Florida Press, Gainesville, Fl.
- Cameron, A., C. D. Thomas, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C.
 Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L.
 Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips, and S. E. Williams. 2004. Will climate change catch us off guard. Conservation In Practice 5:28-29.
- Davis, M. B. 1983. Quaternary history of deciduous forests of eastern North America and Europe. Annals of the Missouri Botanical Garden **70**:550-563.
- Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. Climate Change 15:75-82.
- Davis, M., C. Douglas, R. Calcote, K. L. Cole, M. G. Winkler, and R. Flakne. 2000. Holocene climate in the western Great Lakes National Parks and Lakeshores: implications for future climate change. Conservation Biology 14:968-983.
- Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292**:673-679.
- Drake, F. 2000. Global warming: the science of climate change. Oxford University Press, London, UK.

- Etterson, J. R. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. II. genetic architecture of three populations reciprocally planted along an environmental gradient in the Great Plains. Evolution **58**:1459-1471.
- Etterson, J. R., and R. G. Shaw. 2001. Constraint to adaptive evolution in response to gobal warming. Science **294**:151-154.
- Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford.
- Gitlin, A. R., C. M. Sthultz, M. A. Bowker, S. Stumpf, K. L. Paxton, K. Kennedy, A. Munoz, J. K. Bailey, and T. G. Whitham. 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conservation Biology 20:1477-1486.
- Hannah, L., G. F. Midgley, and D. Millar. 2002. Climate change-integrated conservation strategies. Global Ecology & Biogeography 11:485-495.
- Hansen, A. J., R. P. Neilson, V. H. Dale, C. H. Flather, L. R. Iverson, D. J. Currie, S. Shafer, R. Cook, and P. J. Bartlein. 2001. Global change in forests: responses of species, communities, and biomes. BioScience 51:765-779.
- Hanski, I. 1998. Metapopulation dynamics. Nature 396:41-49.
- Hunter, M. L., Jr. 1999. Forest Ecosystems. Cambridge University Press, Cambridge, UK.
- Johnstone, J. L., and F. S. Chapin. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Global Change Biology **9**:1401-1409.
- Jump, A. S., and J. Penuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8:1010-1020.
- Keel, B. G. 2005. Assisted migration. Page 36 in M. Allaby, editor. Oxford dictionary of ecology. Oxford University Press, Oxford, UK.
- Kolb, A., and M. Diekmann. 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology **19**:929-938.
- Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. Journal of Ecology **90**:68-77.
- Loope, L. L., and T. W. Giambelluca. 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. Climatic Change 39:503-517.

- Luken, J. O., and J. W. Thieret 1997. Assessment and management of plant invasions. Springer-Verlag, New York, N. Y.
- Mackinlay, L., and D. Mardon. 2005. Ben Lawers: a new future for Scottish botanical icon. Plant Talk **41**:22-26.
- Madigosky, S. R. 2004. Tropical microclimatic considerations. Pages 24-48 in M. D. Lowman and H. B. Rinker, editors. Forest canopies. 2nd edition. Elsevier Academic Press, Burlington, MA.
- Martin, P. H. 1996. Will forest preserves protect temperate and boreal biodiversity from climate change? Forest Ecology and Managment **85**:335-341.
- McCarty, J. P. 2001. Ecological consequences of recent climate change. Conservation Biology **15**:320-331.
- Nadkarni, N. M., and R. Solano. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. Oecologia **131**:580-586.
- Neilson, R. P., L. F. Pitelka, A. M. Solomon, R. Nathan, G. F. Midgley, J. M. V. Fragoso, H. Lischke, and K. Thompson. 2005. Forecasting regional to global plant migration in response to climate change. BioScience 55:749-759.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature **421**:37-42.
- Pastor, J., and W. M. Post. 1988. Response of northern forests to CO2 induced climate change. Nature **334**:55-58.
- Penuelas, J., and M. Boada. 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Global Change Biology **9**:131-140.
- Perry, D. A., J. A. Borchers, S. L. Borchers, and M. P. Amaranthus. 1990. Species migration and ecosystem stability during climate change: the below ground connection. Conservation Biology 4:266-274.
- Pitelka, L. F. 1997. Plant migration and climate change. American Scientist. 85:464-473.
- Primack, R. B., and S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology **6**:513-519.
- Ramsay, M. M., and J. Stewart. 1998. Re-establishment of the lady's slipper orchid (*Cypripedium calceolus* L.) in Britain. Botanical Journal of the Linnean Society 126:173-181.

- Rasmussen, H. N. 2002. Recent developments in the study of orchid mycorrhiza. Plant and Soil **244**:149-163.
- Ritchie, J. C. 1986. Climate change and vegetation response. Vegetatio 67:65-74.
- Schwartz, M. W., S. M. Hermann, and P. J. van Mantgem. 2000. Population persistence in Florida Torreya: comparing modeled projections of a declining coniferous tree. Conservation Biology 14:1023-1033.
- Shafer, S. L., P. J. Bartlein, and R. S. Thompson. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. Ecosystems 4:200-215.
- Sturm, M., C. Racine, and K. Tape. 2001. Climate change: increasing shrub abundance in the Arctic. Nature **411**:546-547.
- The World Conservation Union/Species Survival Commission (IUCN/SSC). 1995. Reintroduction Specialist Group guidelines for reintroductions. Gland, Switzerland. Available from http://www.iucn.org/themes/ssc/sgs/rsg/rsgcdrom/PDFs/English.pdf (accessed January 2005).
- Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. Conservation Biology **8**:373-378.
- Thrall, P. H., J. J. Burdon, and B. R. Murray 2000. The metapopulation paradigm: a fragmented view of conservation biology. Pages 75-95 in A. G. Young and G. M. Clarke, editors. Genetics, demography and viability of fragmented populations. Cambridge University Press, Cambridge, United Kingdom.
- Walther, G.-R. 2004. Plants in a warmer world. Perspectives in plant ecology, evolution and systematics **6**:169-185.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.
- Woodward, F. I. 1987. Climate and plant distribution. Cambridge Uni. Press, Cambridge, UK.