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4. GENETIC RESOURCES AND CHANGING ENVIRONMENT

Genetic implications for forest trees of increasing levels of greenhouse gases and UV-B radiation

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Introduction

Globally, the environment is changing and deteriorating as greenhouse gases such as carbon dioxide (CO_2) and tropospheric ozone (O_3) continue to increase at a rate of about 1% per year (Keeling *et al.* 1995, Chameides *et al.* 1995). The increase in these gases is directly related to anthropogenic activities (Chameides *et al.* 1995, Mooney *et al.* 1991) and is likely inducing subtle but substantial changes in the earth's surface temperatures and weather (Cha 1997; Martin 1996). In addition, anthropogenic activities have been linked to decreasing levels of stratospheric O_3 and concomitant increases in ultraviolet-B radiation (UV-B) passing through to the earth's surface. Thus, man is creating a constantly changing global environment for which tree breeders must attempt to develop genotypes and races suitable for future forests. The purpose of this paper is to examine the genetic implications for forest trees of increasing greenhouse gases and UV-B and to suggest where tree breeders need to be concerned about the changing environment. Since very little is known about the impact of greenhouse gases and/or UV-B on genetic population structure, we will not discuss population structure or the effects of selection on population structure.

1. Co-occurrence of stresses

Increasing CO_2 is a global phenomenon with similar increases being observed around the world. In contrast, increases in tropospheric O_3 and decreases in stratospheric O_3 are regional in nature and more patchy (Miller 1993). Thus, future forests are not likely to be exposed to all three of these stresses simultaneously (Kickert and Krupa 1990). Complicating the matter further is that some areas will have increased or decreased temperatures, increased or decreased drought conditions, or increasingly extreme weather

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conditions. Thus, it is difficult to predict the suite of environmental conditions under which populations will function, and it is equally difficult to predict the impacts of changing global conditions on the genetics of forest trees.

2. Genetic consequences of individual stresses

2.1. CO_2

The pre-industrial concentration of atmospheric CO_2 is expected to double in the next thirty years (Barnola *et al.* 1995). This is may trigger a global mean temperature increase of about 2 to 3°C above the pre-industrial baseline (Kelly 1990). Thus, there are two major concerns about the impacts of elevated CO_2 on the genetics of forest trees: (1) natural selection for CO_2 responsiveness, and (2) adaptability to changing climate.

Firstly, trees respond in varying degrees to elevated CO_2. While there is a general stimulation of growth and productivity with increasing CO_2 (Eamus and Jarvis 1989; Körner 1995), some species have minimal responses to elevated CO_2 while others are stimulated dramatically. Similarly, there are markedly differing responses within species in response to elevated CO_2 with growth increases ranging from 38 to 68% (Ceulemans and Mousseau 1994). Similarly, water use efficiency can be changed dramatically with increasing for some species and some genotypes as stomatal conductivity is generally decreased in the presence of elevated CO_2. With this strong genetic variability in CO_2 responsiveness, it seems likely that natural selection will occur (Miao *et al.* 1992, Woodward *et al.* 1991). To our knowledge, however, no one has characterized heritability of CO_2 responsiveness in trees and no one has conducted long-term, community-level CO_2 studies to examine genetic change. Reproductive fitness under elevated CO_2 is also largely unknown (Bazzaz and McConnaughay 1992). Certainly, these are important gaps in the current knowledge base.

Secondly, as temperature and soil moisture levels change with increasing atmospheric CO_2, it is likely that subtle population changes will occur. Present techniques available for explaining the cause and possible consequences of global warming permit only broad generalizations concerning both the temporal and spatial scales over which changes are expected to take place (Miller 1993), as these projections are based primarily on large-scale global circulation models (GCM's). While some migration of forest trees is expected with the changing climate, the magnitude of these migrations is largely uncertain (Cha 1997). Conservation of forest genetic resources via preserves is certainly complicated by climatic change (Martin 1996), as reserves with suitable climate today may not have a suitable climate in 50 to 100 years.

2.2. Ozone

Background global tropospheric O_3 concentrations are increasing at a rate of about 1 to 2% per year (Chameides *et al.* 1995; Finlayson-Pitts and Pitts 1997). A highly phytotoxic compound, O_3 negatively affects trees in many ways including decreasing photosynthesis, accelerating foliar and branch senescence, and inhibiting growth (Pye 1988; Hogsett *et al.* 1997; Chappelka and Samuelson 1998). In eastern North America, the annual mean aboveground growth loss due to elevated O_3 is currently estimated to be in the range of 0 to 10% (Chappelka and Samuelson 1998), but it appears to be more in some sensitive species such as trembling aspen (*Populus tremuloides*) (Wang *et al.* 1986, Hogsett *et al.* 1997).

The impacts of O_3 on forest tree populations has been studied in considerable detail. One of the first such problems to be diagnosed was the oxidant damage to ponderosa pine (*Pinus ponderosa*) over large areas of the San Bernardino Mountains in southern California (Miller *et al.* 1963). Community changes related to natural succession caused by interspecific variability in response to oxidants were initially described in this region by Miller (1973). He noted that mixed forests of ponderosa pine, sugar pine (*Pinus lambertiana*) and white fir (*Abies concolor*) were changing to predominantly fir because of the greater sensitivity of the pines to oxidants. Similar results have been described for Jeffrey pine (*Pinus jeffreyi*) and ponderosa pine at several locations along the western slope of the Sierra Nevadas (Peterson *et al.* 1989, Miller *et al.* 1996).

More recently, similar O_3 -induced population impacts have been noted in the mountain pine forests surrounding Mexico City where O_3 remains at exceedingly high levels (100-200 ppb peaks or more) throughout the year (Miller 1993). In this area, *Pinus hartwegii* appears to be the most highly sensitive to O_3 and has been severely impacted by O_3 since the 1970's (Hall *et al.* 1996) with widespread dieback and decline resulting in its replacement in an extensive forest area surrounding Mexico City.

In the eastern United States, O_3 has been linked to visible foliar injury and growth decrease (Dochinger and Seliskar 1970), decreased reproduction (Benoit *et al.* 1983), and increased mortality rates (Karnosky 1981) for eastern white pine (*Pinus strobus*). Since the responses of eastern white pine appear to be highly heritable, the components are in place for Phase I of natural selection, that is the elimination of sensitive genotypes. Since O_3 sensitive genotypes make up a relatively small portion of natural eastern white pine stands and the selection pressure conveyed by O_3 is rather low (Taylor and Pitelka 1991), the question has been raised does it really matter if we lose these sensitive genotypes. Surely, this remains an openly debated and important research topic.

Similar responses to O_3 for sensitive genotypes of trembling aspen are expected. Evidence for population changes induced by O_3 in trembling aspen in the eastern United States are the studies by Berrang *et al.* (1986, 1989, 1991) which have shown a strong positive correlation between O_3 concentration at the population origin and the mean O_3 tolerance of the population. Populations from more heavily polluted areas tended to be more tolerant of O_3 than did populations from relatively pristine areas. As in eastern white pine, O_3 responses in aspen are highly heritable (Karnosky 1977). Ozone has been shown to decrease aboveground biomass accumulation by 20 to 40% or more for sensitive genotypes (Wang *et al.* 1986, Karnosky *et al.* 1996a, b).

Ozone can also affect the relative abundance of understory vegetation in forests. Barbo *et al.* (1998) showed that O_3 exposures can cause shifts in the competitive interactions between plant species, thereby altering community structure. These understory plant interactions could also influence the ability of forest trees to naturally regenerate, grow and reproduce.

2.3. UV-B

It is well known that stratospheric ozone concentrations have declined during the past 25 years owing to emission of chlorine- and bromine-containing compounds into the atmosphere. This decline has been especially intense since 1984 and is already having important consequences for biological systems. Firstly, a decrease in lower stratospheric ozone concentrations can cool the climate system. Secondly, as ozone naturally absorbs solar ultraviolet (UV) radiation, decreasing concentrations are leading to increasing intensity of UV at the terrestrial surface (Pyle 1997). Documented trends in increasing UV have been strongest at wavelengths within the UV-B (280-320 nm) portion of the spectrum. Cellular processes in biological systems have been shown to be particularly sensitive at wavelengths less than 300 nm (SCOPE 1992).

Forests are long-lived and of critical importance to the maintenance of global cycles, including carbon (C). There are several recent reviews available which summarize known and predicted impacts of enhanced UV-B on various trophic levels within forests (Percy and Gordon 1998, Percy and Cameron 1997, Mcleod and Newsham 1997, Manning and Tidemann 1995, Bornmann and Teramura 1993) to which the reader is referred for in-depth discussion of effects.

It is of concern to long-lived systems like forests that, even under the most optimistic scenarios, stratospheric ozone concentrations are not predicted to recover until at least 2050 (Madronich *et al.* 1995). Deleterious effects have been reported on : 1) physicochemical changes to the first UV-B attenuating barrier, the leaf surface (Gordon *et al.* 1998a,b); 2) photosynthesis, manifested as reduced C assimilation (Sullivan and Teramura 1989), and more negative 13C isotope ratio (Naidu *et al.* 1993); 3) activation of UV-B-absorbing pigments in the epidermis (Schnitzler *et al.*

1996) and trichomes (Shaltsa *et al.* 1994); 4) changes in leaf expansion (Sullivan *et al.* 1996) and morphology (Sullivan *et al.* 1994); and 5) effects on phylloplane fungi (Newsham *et al.* 1997) and foliar saprophytes (Ayres *et al.* 1996).

2.3.1. Genetic implications of UV-B

Assessment of the full impacts of UV-B on genetic variation is not possible at this time. Few experimental response data are available and were largely gathered from short duration (<single season) exposure of seedlings (<2 yrs) to enhanced UV-B at high doses under artificial conditions. Most data, therefore, cannot be extrapolated directly to the field situation. Nevertheless, evidence (Sullivan and Teramura 1992) pointing to the importance of cumulative (several seasons) exposure in determining direction and magnitude of response at the plant level (biomass, growth, C allocation) is building.

The way in which UV-B influences gene expression is yet unclear (Mackerness *et al.* 1997). Based on three lines of evidence, UV-B induced down-regulation of gene expression is stated by the these authors to not be a simple consequence of non-specific damage to DNA.

SCOPE (1992) identified pollination as a potentially UV susceptible stage in plant reproduction. In other life forms such as monocotyledonous and dicotyledonous ephemerals , this ecologically critical developmental stage has been shown to be particularly sensitive to UV-B damage (Musil 1995). UV-B induced damage to the plant genome has also been reported to be inherited by successive generations (Musil 1996). Using fluctuating leaf asymmetry as a variable, the same group later confirmed that accumulated UV-B damage is indeed heritable (Midgley *et al.* 1998).

2.3.2. Cellular and organ levels

Taylor *et al.* (1997) concluded that DNA is the primary absorbing chromophore in the cell in the UV-B region of the spectrum. Although action spectra for DNA indicate maximum absorption at around 260 nm (UV-C), absorption occurs up to 320 nm. Dimeric photoproducts which make up the majority of lesions formed after UV irradiation include cyclobutane pyrimidine dimers (CPD's) and pyrimidine (6-4) pyrimidone photoproducts or (6-4) photoproducts which are toxic and mutagenic (Taylor *et al.* 1997). Major differences exist between monocots and dicots in photorepair of CPD's.

2.3.3. Provenance and species level

As is the case with many stresses, response differs widely between species and groups. Unfortunately, large screenings for within species variance has not occurred with UV-B. Early work by Kossuth and Biggs (1981) on pines showed deleterious effects of UV-B on growth in 5 species, stimulation in 1, and decreases in height for 6 species. Magnitude of effect was species dependent. Sullivan and Teramura (1988) exposed seedlings of 10 pine species and noted stunting or needle discoloration in three. Height was decreased in only 3 species. Biomass increased in 1 species, decreased in 6, while 3 species were unaffected. Gordon, Percy and Riding (1998a), using older seedling material, reported negative leaf surface effects on three of four Picea species tested.

Differences in response are especially large at the life form level. Leaf optical properties, anatomy, phenology and canopy architecture are critical factors influencing group response. Conifer needles attenuate UV-B much more efficiently than do woody and herbaceous dicot leaves (Day *et al.* 1992). Less than 0.5% of UV-B is transmitted by conifer needles, while woody and herbaceous dicots may transmit up to 12% and 41% respectively. UV-B penetration is also much deeper in dicots. Conifers, therefore, are much more efficient and uniform filters for UV-B than other groups (Day *et al.* 1993).

Of prime concern to breeding programs, of course, is origin of parent material. It has been implied for some time that trees growing at higher elevations were more resistant to enhanced UV-B due to naturally higher levels with elevation. Early evidence for this was produced by Sullivan and Teramura (1988) and later corroborated by Binder and L'Hirondelle (1996) using material collected from 5 elevations (850-1700 m). Differences can be partly attributed to needle anatomy (cuticle, epidermis) and pigmentation (Bornmann and Vogelmann 1988) which together influence degree of UV-B light attenuation and depth of penetration within the leaf. The window for damage to sensitive physiological processes in conifers is about 4 weeks during the early part of the needles' first growing season, prior to development of the cuticle/epidermal complex (DeLucia *et al.* 1992).

Latitude is also an important factor. Using loblolly pine (Pinus taeda) seed sources collected from 7 U.S. latitudes (31° to 39°N) selected to mimic a natural UV-B gradient, Sullivan and Teramura (1992) observed biomass reductions in 2 of 7 (28%) sources after one year of field exposure to enhanced UV-B dose. In year two, 50% of sources tested decreased biomass and after three years, 75% of sources had reduced biomass. It is important to note that negative effects were equal in both above- and below-ground portions.

2.3.4. Community level

There have been no stand- or ecosystem-level enhancement experiments conducted. Only one report exists of visible UV-B damage on mature, field-grown trees (Loucks 1994). However, given the large differences which exist in response between life forms and between tree species at the leaf and seedling levels, it is reasonable to conclude that current and predicted UV-B levels pose a real and long-term threat to forest genetic variability and consequently, forest sustainability on a global scale.

State of science suggests that subtle, cellular- and organ-level effects may be occurring now in many forested regions, particularly in forests growing at higher latitudes. These may be leading to impacts on leaf morphology, surface physicochemical characteristics and physiology. Perturbation of essential processes would be expected to result in differential effects determined by species composition, age, phenology and local edaphic conditions.

Alteration of canopy architecture through crown thinning with resultant increased transparency and transmission of damaging UV-B to ultra-sensitive ground flora may have long-term consequences for biodiversity and forest ecosystem structure. Certainly, there are indications that host-pathogen interactions will be affected (Ayres *et al.* 1996). Resilience to UV-B is also diminished in the presence of other co-occurring global stressors such as extreme climatic events (temperature extremes) and increasing atmospheric CO_2 (Yakimchuck and Hoddinott 1994) and tropospheric O_3 (Zeuthen *et al.* 1997).

3. Genetic consequences of interacting stresses

Although little research has been conducted with interacting global change stresses, there are reasons to suggest that genetic responses to multiple stresses will be difficult to predict as is demonstrated in the next few examples. The combination of UV-B and ozone reduces pollen tube growth more than either stress alone (Feder and Shrier 1990). Similar results have been shown for visible foliar injury in eastern white pine induced by SO_2 plus O_3 (Dochinger and Seliskar 1970). Kull *et al.* (1996) found an interesting response when exposing trembling aspen clones to a combination of elevated CO_2 and O_3. While the predicted outcome was for the elevated CO_2 to alleviate the O_3 stress, this study actually found more injury by O_3 when CO_2 was present (Kull *et al.* 1996). The authors speculated that antioxidants may be reduced in the presence of elevated CO_2, as reported by Badiani *et al.* (1997), thereby increasing the O_3 sensitivity of otherwise tolerant genotypes. Antioxidants appear to play a role in determining O_3 tolerance in aspen (Sheng *et al.* 1997). Subsequent growth studies have also suggested that CO_2 did not alleviate O_3 effects in aspen (Karnosky *et al.* 1998).

It is well known that plant responses to elevated CO_2 are very sensitive to nutrition, particularly to nitrogen levels in the soil (Lloyd and Farquhar 1996). Thus, it is likely that regions of the world experiencing high levels of anthropogenic nitrogen input would also be likely places to see the maximum CO_2 effects.

4. Novel approaches to study the impacts of atmospheric pollutants on forest tree populations

4.1. Pollution gradients

Inferences of genetic change can be made from examination of natural pollutant gradients. Berrang *et al.* (1986) first documented genetic differences in *Populus tremuloides* responses to O_3 from populations occurring in low or high O_3 areas. This work was later substantiated from similar results for a larger region (Berrang *et al.* 1989, 1991).

Recently, our team has established *P. tremuloides* clones of varying O_3 sensitivity in plantations designed to address (a) O_3 bioindication by foliar symptom development, (b) growth and yield under differing O_3 seasonal doses, and (c) competition between O_3 sensitive and tolerant genotypes under differing O_3 seasonal doses. The studies were established some five years ago in Rhinelander, Wisconsin (low O_3), Kalamazoo, Michigan (intermediate O_3), and Kenosha, Wisconsin (high O_3). These sites have proven very useful in showing the effects of O_3 on competitive interactions. Severe growth suppression and increased mortality among sensitive genotypes have been documented for the highest O_3 site within the first five years. We have also documented deterioration of the cuticle at the elevated ozone locations and linked this to increasing pest occurrence (Percy, Karnosky and Mankovska 1998). This would suggest that selection pressure is relatively higher than has previously been suggested (Taylor and Pitelka 1991) for the early development of densely populated aspen stands coming in after a fire, clearcut or other disturbance.

Heavily impacted by long-term atmospheric pollutants, the former Eastern bloc countries offer excellent study sites to examine the impact of atmospheric deposition on forest communities. These are sites of large-scale forest ecosystems where pollution loading has resulted in severe forest decline. At one such study point in central Slovakia (Mankovska *et al.* 1989), Karnosky, Mankovska and others are utilizing Müller-Starck's (Müller-Starck 1985) technique of matched pairs of pollution "sensitive" and "tolerant" European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), and silver fir (*Abies alba*) to compare gene frequencies and heterozygosity between sensitive and tolerant populations.

4.2. FACE technology

Scientists have long conducted atmospheric pollutant studies in laboratory, greenhouse or open-top chambers. These chambers have been very useful in characterizing early seedling development, basic physiology of pollution stress, and threshold levels for foliar and growth responses induced by pollution. Because of limited chamber size and because of the ever-present chamber effects, these techniques are not useful for longer term, larger scale research questions dealing with mature forest trees growing in natural plant communities.

Recently, a new technology has developed that allows for entire plant communities and trees of any size to be exposed to elevated CO_2 and/or O_3. Modified from the design originating in England (McLeod 1995), a large scale Free-Air CO_2 Enrichment (FACE) experiment (FACTS I) was established on a 20-year-old loblolly pine forest in North Carolina (DeLucia and Thomas 1995, Ellsworth *et al.* 1995). We have modified the FACTS I CO_2 distribution system to allow for dependable and reliable exposure of both elevated CO_2 and O_3 in an aggrading aspen/birch/maple stand in northern Wisconsin (FACTS II) (Karnosky *et al.* 1995). In this study, we are examining the relative CO_2 and/or O_3 responses (growth and physiology) via interspecific and intraspecific investigations. These studies should help the understanding of forest community responses to elevated levels of greenhouse gases, and they give us a window into what forests will be like in 50 years.

4.3. Molecular approaches

The field of molecular biology is rapidly evolving and many new tools are emerging that will be useful in studying the impacts of atmospheric pollutants on forest tree populations. For example, studies of pollution impact on genetic diversity and of population adaptability to pollution stress will likely be facilitated by emerging molecular marker techniques. While protein electrophoresis remains a useful tool for population biologists, techniques based on nucleic acids such as RFLP, RAPD, and AFLP and SSR (microsatellite) markers offer powerful new tools for analyzing germplasm (Powell *et al.* 1996), examining genetic divergence among populations (Parker *et al.* 1998), and utilizing marker-aided selection.

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