General paper

Getting the species and provenance right for climate change

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Summary

Current predictions of climate change are based on simulations using global circulation models of the atmosphere. Without validation of the results of these models, we have no idea of whether or not their predicted climate changes will take place. Greater effort in determining the accuracy of the models is needed, given that they are the only method currently available to predict the impact of increased CO_2 levels on the climate.

In the absence of proof of current climate change, it would be prudent, for now at least, to consider the predictions of increased average annual temperatures and changes in precipitation patterns. Similar changes have taken place in the past, but the fear now is that these changes will take place more rapidly in the future. The predicted increase in winter temperatures will probably mean less frost damage, but will also affect the date of bud break, which will impact on some species more than others. Genetic variation in traits associated with adaptation to local conditions, such as date of bud break, date of bud set, optimal temperature for photosynthesis, pest resistance and drought tolerance, exists not only at the species level, but also at the provenance, family and individual level. Therefore, by identifying highly adaptable sources of material, it is possible to develop new varieties which will be better able to cope with future climatic conditions than current material. This information is best obtained from classical provenance experiments. Climatic changes will probably result in changes in the natural distribution of forest tree species, and may limit the use of some species in plantation forestry. The impact on Sitka spruce (*Picea sitchensis* (Bong.) Carr.) should be minimal, but a number of other commercially important species, such as Norway spruce (*P. abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), common beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.) and sessile oak (*Quercus petraea* (Mattuschka) Lieblein) may be adversely affected. What is now required is validation that the current models are correct, followed by a commitment, together with a plan, to do something about those species at greatest risk.

Introduction - should we believe the models?

Although climate change seems to be something we have been hearing about for the last 10 years or so, it is not something new. It has been taking place almost since the formation of the earth. Indeed, the climate of Ireland for over 90% of the last 2.5 million years has been very cold, with an average air temperature 6°C colder than today (Coxon, 1997). The current problem arises from the unprecedented rapidity of the present predicted change. In fact, it has been suggested that dramatic changes in the climate will take place during the rotation length of a single crop (Schmidtling, 1994). Such rapid change will very likely put some species and seed sources at risk.

During the last 30 years, a variety of changes in the climate have been predicted, but

for different reasons. In the 1970s, natural global cooling was predicted to result in a new ice age, while in the 1980s, the threat of global nuclear war led to predictions of "nuclear winter" (Coxon, 1997). Now in the 1990s, the main concern is global warming, or perhaps more accurately, climate change, resulting from increased CO_2 emission.

Climate change predictions are based on increased levels of atmospheric CO_2 incorporated into global circulation models (GCM) which are based on physical conservation laws to predict future environments. Depending on the initial inputs, a set of new conditions are calculated using the models which provide the basis of subsequent conditions. For this reason, very slight alterations either in the initial conditions or in the model itself can have a profound effect on the results. In addition, as these models employ a relatively large grid area (5° latitude x 5° longitude), they do not allow for predictions of climate changes at the local level (Loehle and LeBlanc, 1996).

The scientific method operates on observations of nature which are used to develop hypotheses which are then tested. Hypotheses which are consistent with new observations are accepted as long as they agree with the data, while hypotheses that do not are rejected. Mathematical models are a way of studying complex systems and developing hypotheses for testing. Such hypotheses should be subject to testing and either accepted or rejected, but if not testable or not tested, they should not be assumed to be correct. For a model to be useful, it must be accurate in its predictions of future conditions when compared with actual observations. Unfortunately, such validation based on observations of climate change are not currently possible (Hanninen, 1995). The use of GCM models, which have been described as "greatly simplified models" (Loehle and LeBlanc, 1996), to make predictions of a future earth's climate without validation, may be giving us very inaccurate results. A good discussion of the limitations of models to predict future climate changes is made by Reifsnyder (1989).

Future climatic conditions

Nevertheless, for the purposes of this discussion, the predictions of changes in the climate based on current models will be assumed to be correct. Basically, these models predict a doubling of CO_2 levels by the year 2050, resulting in an increase in average world temperature of between 1.5- 4.0°C (Loehle and LeBlanc, 1996). In addition, warmer night temperatures and warmer winter temperatures are anticipated. Sweeney (1997) has provided information on what specific changes may occur in the Irish climate, which include an average annual temperature increase of 1.0°C, an average winter temperature increase of 0.5°C, and an average summer temperature increase of 1.5°C. Changes in national precipitation rates are also predicted, but local changes are very difficult to predict. Although predictions in future precipitation patterns are less accurate, it is expected that there will be little overall change in annual precipitation in Ireland, with a 5-10% increase in average winter rainfall and a 5-15% decrease in average summer precipitation.

The implication of these changes in climate on forests has received much attention. Warmer winters may result in increased respiration, increasing stress levels in conifers (Loehle and LeBlanc, 1996). Warmer winter temperatures may also prevent species from fulfilling their winter chilling requirements (necessary for dormancy release), alter flowering times, seed production and seed germination (and thus natural regeneration rates), affect insect and disease levels (warmer winters may mean lower winter mortality rates as well as more insect generations/year), and increase summer drought stress (Ledig and Kitzmiller, 1992). In light of these possible changes, we now need to consider if and how

forest tree species will be able to cope with them.

Adaptation

If such changes in local climate do take place, they will have an effect on the species as well as the provenances or seed origins that we plant. Species trials are designed to identify species which are best adapted to local conditions. Provenance experiments identify patterns of variation within a particular species, and allow the identification of the best sources of seed for local use (Ledig, 1991). Although it is usually assumed that a species range is determined by climatic conditions which limit where a species is able to survive, this assumption is not true (Loehle and LeBlanc, 1996). A large number of 'exotic' species have demonstrated more vigorous growth in environments very different from their natural locations, due to their ability to adapt to the new conditions (Beuker, 1994). This ability to adapt to new environmental conditions results from genetic variation within the species.

The belief that every individual within a species has identical environmental limitations and tolerances is not correct (Ledig, 1991). Genetic variation in traits relating to the ability to adapt to different environments, such as date of bud break, date of bud set, optimal temperature for photosynthesis, drought tolerance, pest resistance and ability to compete (Perry, 1979), result in differences in adaptability in different species, provenances, families and even clones. Even in very poorly adapted species or provenances, rarely is there a complete failure. Usually a few individuals will survive. They may not thrive and reproduce, but some do have the ability to survive. Adaptability thus permits an individual to endure a much broader range of environmental conditions than it would normally encounter. The fact that most forest trees contain considerable amounts of genetic variation helps to makes them very adaptable (Eriksson *et al.*, 1993).

The belief that natural selection produces individuals most suitably adapted to local conditions has led to the incorrect assumption that local material is best. As selection is only for individuals that will survive and reproduce under local conditions, there is no need for optimal adaptation to local conditions. Nature is not interested in optimisation, so maximum fitness to a particular environment simply does not exist (Eriksson *et al.*, 1993). Adaptation is conservative so that selection is made for the fewest traits needed for the individual to survive and reproduce in the new environment. As a result of this very conservative natural selection, most individuals fail to take full advantage of the local environment. Selection for protection against late spring frosts by late bud break may result in a loss in the ability to take advantage of the full growing season. The transfer of provenances or origins from mild conditions may increase their ability to more fully utilise the growing season, but they may be at an increased risk of damage due to late spring or early autumn frosts (Ledig and Kitzmiller, 1992).

In addition to genetic variation in adaptability at the species level, adaptation also occurs at the provenance level, at the family level and at the individual level. To focus on provenance as the best genetic leverage point to cope with climate change is perhaps too simplistic. At the individual level, several late flushing (late May) rapid shoot elongating clones of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) have been identified in clonal trials. This behaviour has not been observed at the family or provenance level, even though these individuals probably exist. For this reason, the original title of this paper has been altered from "Getting the provenance right for climate change" to "Getting the *species and* provenance right for climate change".

Getting the species right

Although it may appear at first that a major benefit of increased average annual temperatures would be a reduction in frost damage, another aspect of winter cold may play a pivotal role. A series of studies on 15 UK species (Cannell and Smith, 1983; Murray *et al.*, 1989) showed that an increase in average winter temperatures resulted in a delay in bud burst for many species. This was due to the fact that trees require a certain number of chilling hours (hours below +5°C) in order to be able to break bud when conditions permit in the spring. An increase in average winter temperatures would lead to a delay in accumulating the necessary number of chilling hours, thus delaying bud break. Different species have different chilling requirements, as reflected in variations in the average date of bud break between species (Kramer, 1994). Data on the variation in the chilling requirements of different species (Table 1) has been used in modelling the impact of climatic warming on both the probability of spring frost damage (Kramer, 1994) and the adaptive ability of northern European forest tree species to both current and future climatic regimes (Sykes and Prentice, 1995; Sykes *et al.*, 1996). Species which require a long rest period (below +5°C) would be most affected by warmer winter temperatures.

Table 1. *Differences in duration of the rest and the quiescence periods (days) in different European tree species (Kramer, 1994).*

Species	Rest requirement	Quiescence requirement
European larch (*Larix decidua* Mill.)	101	65
Downy birch (*Betula pubescens* Ehrh.)	105	64
Common beech (*Fagus sylvatica* L.)	128	50
Pedunculate oak (*Quercus robur* L.)	126	56
Sessile oak (*Q. petraea* (Mattuschka) Lieblein)	139	50
Common ash (*Fraxinus excelsior* L.)	149	39
Norway spruce (*Picea abies* (L.) Karst.)	117	72
Scots pine (*Pinus sylvestris* L.)	122	68

These projected species responses to global warming suggest that the climatic conditions resulting from a doubling of current CO_2 levels by the year 2050 could result in dramatic changes in the adaptability of several commercially important species to the new climatic conditions in Ireland. It appears from a comparison of current and future species distribution patterns (Sykes and Prentice, 1995; Sykes *et al.*, 1996) that Norway spruce (*P. abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), common ash (*Fraxinus excelsior* L.), common beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Mattuschka) Lieblein) may not be as successful under a warmer Irish climate, due to increased competition from better adapted species. This assumption is, however, based on overall species requirements, and does not take into consideration natural genetic variation in chilling requirements possible at the provenance, family or even individual level.

Interestingly, for Sitka spruce, average warmer winter temperatures on lowland sites would result in bud break at a slightly later date than that under current conditions (Murray *et al.*, 1989). A delay in bud break might slightly reduce the probability of damage by late spring frost, but would also reduce the length of the growing season. On colder upland sites, where the effect of increased average winter temperatures would be less, there would be less of a delay in the date of bud burst than on the warmer lowland sites (Murray *et al.*, 1989). The same would be true for Norway spruce, Scots pine, common ash, common

beech and sessile oak. On cool upland sites, these species would be more adversely affected by warmer winter temperatures than on lowland sites.

Getting the provenance right

Provenance experiments provide valuable insights into the performance of different seed sources from the entire species range (Matyas, 1994; Schmidtling, 1994). In Sitka spruce, if bud break is delayed as a result of a warmer winter climate, it then becomes important to use provenances which will take full advantage of the reduced growing season. Certainly the more southerly provenances such as Washington and Oregon, which begin to set bud in late October or November, would be more productive than Queen Charlotte Island material, which sets bud in late August or September.

Provenance experiments with Norway spruce (Krutzsch, 1992) have shown that this species is very adaptable to a wide range of sites. Across 10 European trial sites, the southeastern sources from the Carpathian and Bihor Mountains in Romania have consistently performed the best. As Norway spruce is basically a continental species, it does tend to have problems in exposed oceanic conditions, one example being the 'top-dying' syndrome observed in Ireland, Scotland and Denmark. With increases in winter temperature resulting in higher winter respiration rates and an increased likelihood of summer drought, the Romanian provenances of Norway spruce in Ireland may be exposed to conditions to which they are unable to adapt. A provenance experiment involving 1,100 Norway spruce provenances planted on one site in 1968 has already provided information on the date of bud break and the growth and form of the species from all parts of its natural range. This information should help in identifying the best adapted seed sources.

In Scots pine, the situation is different, with local material usually outperforming any other provenance (Giertych, 1979). Currently, the recommended seed sources of Scots pine for Ireland are Scottish provenances. With an increase in average temperatures and drought, more eastern sources may, however, prove to be better adapted. Unfortunately, the only provenance experiments with Scots pine in this country are limited to Scottish and Norwegian provenances.

Results from a beech provenance trial planted in 1995 has already shown that eastern provenances (Slovakia and the Czech Republic) and high elevation provenances break bud first, while western provenances (Dutch, French, British and Irish) are the last to flush. While early bud break could result in rapid height growth, it is also at greatest risk to late spring frost damage. Thus, while western European sources of beech may be most tolerant to late spring frosts, they will flush late in the spring under warmer winters, and will therefore be less able to compete with other species.

Regarding oak, an IUFRO oak provenance trial comprising Irish, British, French, Dutch and German provenances, was planted in 1990. Once again, the Dutch, British and Irish provenances were the last to break bud. As with beech, late flushing could become a liability with warmer winters.

There have been no provenance trials comparing common ash from Ireland with any other seed sources. While it has always been assumed that Irish ash is best, as shown in the examples of beech and oak above, warmer winters may result in later flushing and thus, reduced growth and productivity.

What are others doing about it?

Concerns about climate change have been expressed by tree breeders in other parts of the world, such as New Zealand and Canada. In New Zealand, the major species, Mon-

terey pine (*P. radiata* D. Don), prefers a moist, warm site for optimal growth. These conditions are also optimal for fungal growth which could result in increased disease problems. Higher levels of CO_2 could increase pine growth rates and may also increase the nutrient requirements of the species. Increased storms would increase the amount of wind damage, thus reducing the volume of marketable timber (Grace *et al.*, 1991).

The New Zealand Monterey pine breeding programme can produce a new variety of pine in 12-14 years. This may be rapid enough to develop new varieties adapted to the changes in the climate. Results from tree improvement tests in New Zealand suggest that good individuals will do well on a range of sites, creating the opportunity to develop good, all-round performers which should do well even under altered environmental conditions. There are, however, limits to genetic variation in any species, and alternative species may be necessary for sites which are no longer suitable for Monterey pine (Grace *et al.*, 1991).

Tree improvement work with black spruce (*P. mariana* (Mill.) Britten, Sterns and Poggenberg) in Canada has employed screening of genetically improved material in growth chambers under predicted environmental conditions. Results so far show that black spruce material selected for good growth under current conditions will do well under future conditions (Wang *et al.*, 1994).

Other work in Canada has suggested that some alterations in the mixture of the major species may be necessary to cope with projected environmental changes. Shorter rotation length species would provide the greatest flexibility. In addition, hybrids between native and introduced species, such as hybrid larch (*Larix* x *eurolepis* Henry), might be an option (Fowler and Loo-Dinkins, 1992).

Other options

The uncertainly of whether or not dramatic changes in the climate will occur suggests caution in making radical changes in species and provenance selections. If provenance changes are to be made, one interesting suggestion is to mix material from both currently used provenances and provenances believed to best match future conditions (Ledig and Kitzmiller, 1992). Similarly, selected species mixtures might be a good option, to ensure continued forest productivity in a changing climate. We need to look closer at Norway spruce, Scots pine, common ash, common beech and sessile oak, to determine whether or not they will actually be at risk, as suggested by some researchers.

Should breeding programmes immediately embark on breeding material specifically designed for future environmental conditions? In light of the fact that future environmental conditions can not be accurately predicted, this would be a difficult task. There are two options: breed for specialist varieties designed specifically for future conditions; or breed for generalists which have the adaptive capacity to cope with uncertainty. From the evidence from New Zealand (Grace *et al.*, 1991) and Canada (Wang *et al.*, 1994), it appears that improved material selected for good growth under current conditions may provide a reasonable base from which to develop more general purpose adaptable varieties for the future.

Conclusion

The assumption that global circulation models currently available are capable of providing accurate predictions of the climate 50 years into the future, is a large one. Models are tools for the generation of hypotheses which need to be validated in light of observed data. Validation of these models will require time, but until validated, these models need

to be viewed with some scepticism.

In the absence of validated models, we can only assume that they may be correct and consider the implications of the climatic changes they predict. For Ireland, slightly warmer average winter temperatures and increased average summer temperatures (Sweeney, 1997) will have important implications on the completion of chilling requirements in a number of species. Some species, such as Norway spruce, Scots pine, common ash, common beech and sessile oak, may be less productive and subject to greater competition in the predicted Irish climate. Although this premise ignores the fact that significant genetic variation in adaptive traits exists in all species at the species, provenance, family and individual level, this does provide a short list of species for immediate attention.

Current and future provenance trials should be useful in identifying seed sources which may be better able to cope with a reduced chilling period, perhaps by moving from native or naturalised sources to more southerly material. Although provenance experiments can be a very long-term activity, results from a recently established (1995) beech provenance trial have already provided information on the pattern of bud break in the species which will perhaps be most affected by climate change. This illustrates that provenance experiments can provide useful information in both the short and long term, depending on the traits of interest. Very limited information on provenance is available on Scots pine in Ireland, and no specific information is available on sessile oak or common ash. It may be possible to access information from other provenance experiments in Europe, to identify sources of highly adaptable provenances or families for testing under Irish conditions.

It is also possible that evidence from other tree improvement programmes is correct, and that material which has been genetically improved (selected and tested) under current conditions will also be well adapted to future conditions. If this is true, we should initiate or accelerate our tree improvement efforts in those species at risk.

Natural genetic variation will provide the range of adaptive traits necessary to combat the potential influence of climatic changes in the future. Techniques exist to attack these problems. Perhaps what is most needed now is both clear evidence that the climate is changing, followed by a strong commitment that something needs to be done to offset the effect of these changes on Irish forests.

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