DISCUSSION RELATING TO SESSIONS I and II

Polk: I would like to ask Dr. Miksche whether he suspects or can surmise any relationship between abundant redundancy of DNA in *Pinus* spp. and reported poor performance of pine polyploids?

Miksche: You are relating polyploidy to redundancy? This is what you are asking essentially? I think polyploidy is one manifestation of redundancy—it probably acts in the same way in an evolutionary sense in that DNA has been increased. When working with conifers, however, we do not normally have polyploidy. At least among our subject species we don't have it. This increase in DNA through redundancy is working in the same way as in polyploids. It provides an adaptation method, and we think of it as a means of extending the chromosomes. It seems probable that changes in redundant DNA can increase or decrease heterochromatin and not euchromatin, which, in the main, is the basic Mendelian DNA. Some people like to call heterochromatin junk, but it isn't. It does code, and it does do some work. In terms of your question on polyploidy and what is happening in the conifers, the same thing is happening. It just happens that in the angiosperms there is a greater manifestation of the amount of increase in DNA as a result of adaptation and evolution working on polyploid systems. In general, conifers have adapted in such a way that they have been able to increase and decrease DNA without utilizing polyploidy as a factor. Of course, I am talking about extant species and not about the evolution of basic genomes over the long scale of time.

Miksche: While I have the floor, I would like to ask Dr. Carpenter to please reiterate: Did you find that in quantifying your chlorophyll content per cell that there was a difference or any kind of latitudinal relationship?

Carpenter: No, in the manner in which I took data, I found no relationship. I was a little surprised, because, in the materials we had, the leaves of southern sources had not begun to abscise whereas they had in northern representatives. Although I did get some minute differences in photosynthetic efficiency, there was no significant difference.

Miksche: I was hoping that you would find a relationship between chlorophyll content and photosynthetic efficiency, because then the next step would be to determine the amount of DNA per chloroplast, and that would be a manifestation of redundant DNA, and you would have the same picture—probably a circular type of DNA.

Carpenter: I have followed the literature over the years trying to relate this, and perhaps ninety percent of the cases show no relationship between chlorophyll content and actual rates of photosynthetic activity.

Miksche: Actual rates of photosynthetic activity on a per cell basis?

Carpenter: Not on a per cell basis, no. I can't figure that. We were dealing with whole plants.

Polk: Walnuts have been variously reported as being dichogamous and, perhaps, apomictic. I would like to ask Dr. Beineke if, in his efforts to breed *Juglans nigra,* he has observed or had cause to suspect either of these variants in the regeneration process?

Beineke: Dichogamy does occur, and, theoretically, this is the way that outcrossing occurs in black walnut. Unfortunately, according to my observations, weather or normal overlapping of male and female flowering on a tree does allow for selfing. Therefore, in some years, inbreeding can be abundant. Insofar as apomixis is concerned, I have no idea concerning its occurrence in black walnut.

Shreve: On this matter of apomixis in walnut: Professor Joseph Sobeck at the University of Prague in Czechoslovakia has developed two apomicts of *Juglans regia.* We have some of these growing in our seed orchard at Kansas State University. We have not had them long enough, however, to test their performance as apomicts.

Brunk: I would like to ask Walt Beineke a question. Walt, we don't seem to be getting in Missouri the same thing that you are getting in Indiana in natural regeneration of black walnut. When we remove, in a timber sale for example, an old tree, there is frequently an enormous amount of walnut regeneration around the old tree. This is either advance walnut regeneration, or an abundance of seedlings comes in shortly thereafter. Do you feel that you have a local isolated situation in Indiana? In many cases in natural stands in Missouri, black walnut is almost like a weed in that we have over-stocking of vigorous young trees. We have considerable difficulty in convincing people to thin young stands in those instances where walnut itself is a major competitor of more desirable young walnut trees. This is particularly true in southwestern Missouri. Do you feel that what you describe is a local problem in Indiana, or do you feel that such conditions are widespread?

Beineke: I am not certain as to whether or not this is a local condition in Indiana. What I have described is a general observation. In some areas, however, we do have the same circumstances you describe for Missouri—an excess of reproduction, causing overstocking. There are other places, however, where we have virtually no reproduction; or, if we do have walnut seedlings, they seem to be outcompeted by other species. Let us put it this way: on better sites, generally speaking, it is tough to get the walnut to stay there. I do recall areas that I have been in Missouri—last year, for instance, during the meeting of the Walnut Council—where there seems to be a fairly continuous population of black walnut. You do not have the breaks such as we have in central and northern Indiana, with virtually miles between woodlands. In other words, in Indiana we are getting more isolated blocks of trees and, therefore, more related matings. I am not going to say that our problem is attributable primarily to selfing, but we do have related matings which bring about reduced vigor.

Funk: I have a question for Stan Carpenter. I am curious about the apparent inconsistency between the tendency for black walnut from southern seed sources to grow faster than northern origins, according to our tests, and your finding that southern sources have fewer or at least smaller leaves and apparently little difference in stomatal measurements. Are you ready to speculate that southern sources have a greater internal efficiency?

Carpenter: I didn't report growth findings, but my data on growth do agree with yours, i.e., southern sources do outperform. I was surprised at the lack of a positive relationship between leaf area and growth rate. The only thing that I am willing to say is that obviously other factors are involved, i.e., factors other than stomatal differences and leaf sizes. I am perhaps destroying some of my premise, but I do feel that stomates and their distribution are important, but that is not the entire answer. We are doing labelling now within those southern sources that grow faster. I think that relative growth rates will eventually be explainable in terms of various factors such as the length of growing season, dormant seasons, and other variables for which we have not yet accounted.

Teich: I would like to direct a question to Howard Kriebel and, also, to the group at large. One of the major problems in heritability studies is that heritabilities seem to drop with age. Dr. Kriebel recently published a paper, I believe, in which he suggested that this perhaps was accountable to changes in genetic variances and error variances. The paper he gave today touched on that, but he also said that the change with age appeared to level off somewhat. Based on some other studies at Rhinelander, it appears that early performance often indicates later performance. There have been still other studies in which early performances and later performances are very closely correlated. I have come across a problem in white spruce in which I looked at 11-year-old and 18-year-old results. In this study, results at these two age spans were similar, but I found a strong drop in heritability. In other words, the fastest growing material has continued to be the fastest, but differences have decreased. Now for the question: Are these relatively strong estimates of heritability obtained at early ages due to real genetic differences; or are they brought about by such other variables as seed size and nursery bed differences, giving certain seedlots an early advantage that they will retain for a number of years?

Kriebel: Regarding seed size, this is why we included reciprocal crossings. Presumably, seed size or weight can be a main aspect of maternal effects. I don't think the results I reported today were due to that. We did, as I mentioned, try to closely control the environment and, thereby, keep environmental variance at a minimum. We expected, therefore, to get a situation that you would not find in the field. We felt that the decline of heritability was not due to an actual decrease in additive components but due to an increase in error variance. I think the key point is that when you make a shift in environment you then upset the relative importance of genetic and environmental effects. At the time of transplanting you have these big changes. The thing that surprised me was that when we put them out in the field, we didn't get a continuation of this reduction. It remained constant—apparently due in part to the more efficient field design but perhaps also to outplanting in paper pots, thereby keeping the root systems intact and relatively little distrubed. At age four years, as you noticed, there was quite a shift in relative sizes of the components of variation, bringing about an increase in the estimated heritability.

Jokela: I would like to attempt a partial answer to Tiech's question. Some years ago I studied heritability on height growth at one month, two months, and three months of age. There was, as I recall, a definite drop in estimates of heritability, even though we had not moved the seedlings. This was followed by a further drop in heritability two or three years after transplanting. I hope to get still another estimate at age ten years from seed.

Kriebel: I should have mentioned that in this test and in other tests, when we held the seedlings without transplanting, the variances remained rather constant. But, when we lifted them and put them in a nursery or repotted them and put them in the field, we got a change.

Nienstaedt: I can comment on Teich's question too. You may not have noticed the heritability estimates that I showed for heights in the nursery. The one for 1970 was about 0.21 and for 1971 around 0.41. There again, I think it was because in 1970 there still was the effect of environmental changes from lathhouse to nursery. By the time the seedlings got established again in the nursery, we were back at the level of heritability estimates previously realized on the basis of growth room and greenhouse data.

Kriebel: I think you can get even higher estimates if current-year growth is used, because there is less effect of pre-transplanting environment on current height than on total height.

Schantz-Hansen: I would raise a question with those who have been commenting on heritability estimates: Would you expect a trend in heritability to revers, itself? In other words, could it not be true that those trees with a relatively poor early performance prove to be the best by, say, age 40?

Brunk: Don't some southern pine data show this? As I recall, some of Wakeley's data show this. Some loblolly and slash pines that proved superior at age 15 were no longer among the best trees at age 30. He found that only 20-some percent of the superior trees at age 30 could have been predicted at age 15. The percentage went up a little by age 20, but Wakeley recommended, I believe, that one should not base any prediction of superiority on any trees less than 25 years old in those particular species.

Kriebel: Nanson of Belgium has reworked some of those data and doesn't agree with Wakeley's results.

Brunk: Well, that is interesting, isn't it?

Cunningham: I have a question that concerns the paper by Ying, Schultz, and Bagley. You mentioned that you did not think you were getting much crossing between some of the graft clones. Have you looked at flowering time?

Bagley: We don't have any data that will depict accurately any such differences. Some observations have been made on time of flushing in the spring, including flowering time. We have not conducted a careful study, however, on flower phenology. There are some differences though.

Cunningham: I would like to ask Dr. Farmer what he means by "super cooling?"

Farmer: In this case I mean reducing the temperature to a point slightly below the freezing of water (32° F.) but not below the point at which ice is formed in the acorns.

Farmer: I would like to ask Nienstaedt a question on dormancy and chilling requirements. We have noted in a number of forcing studies that material from southern sources generally responds more rapidly to forcing than that from northern sources. Are there not two components of this difference? First, there is the general trend from north to south, with the northern material requiring more chilling than that of southern origin. Then, there seems to be a second component of variation associated with spring climate. Spring climate toward the middle of the range might be more variable than either the northern end or the southern end. Therefore, we get a response in the middle of the range that would bring about a greater chilling requirement than at either the northern or southern parts of the species range. Such a longer chilling requirement would act as a safety factor. This would also apply to altitudinal variations. Do you have any data that might indicate this is true?

Nienstaedt: This would have no relationship to the material I presented today, because all of the early and late individuals came from one population. To answer your question, however, I believe the thesis you propose is a good one. There is a paper by G. B. Sweet that argues that precise point. Based on observations on Douglas-fir, he came to the same conclusion that you have described.

Farmer: Randall or Jokela may have information from the provenance study of *Populus deltoides?* Was it not the trees of Minnesota and Louisiana origin which came out first, with trees from the middle latitudes flushing later?

Randall: Louisiana sources were the earliest, followed by those from Minnesota and Wisconsin. Origins from latitudes in between came out about 5 to 7 days later.

Nienstaedt: There appears to be quite a difference between genera, or between species within a genus. I don't know what to make of it. Take some of the southern hardwoods such as *Liriodendron, Liquidambar,* and *Platanus—and,* in part but not entirely, *Populus deltoides—southern* sources flush first. In most northern conifers and some hardwoods, such as yellow birch, northern sources flush first. So, there are two opposing trends, with differences found between groups of species. Such differences may perhaps be explainable in terms of the evolution and migration histories of species.

Farmer: Two processes may be involved here. One is chilling which brings plants into a state of imposed dormancy. Secondly, there may be different temperature relationships after plants are in a state of imposed dormancy. A northern race, even though in a state of imposed dormancy, may begin growth at a lower temperature than a southern one. Conversely, a southern race in a state of imposed dormancy would begin growth later when at this cooler temperature. Do you see what I am getting at?

Nienstaedt: I am not .sure I see what you are getting at? I think we must make a very definite distinction between chilling requirement and subsequent growth. Chilling requirement, at least for northern species, is usually fulfilled by the middle of winter. For example, adequate chilling of white spruce has occurred by late December. There is no further chilling requirement for that species beyond that date, and I think this will apply to most species. After that date we are talking about responses to increasing temperatures the following spring.

Farmer: This suggests that the whole process needs study in a series of growth chambers.

Kriebel: In sugar maple, the chilling requirement of northern ecotypes is not reached until mid-February, if normal growth is to follow. You can get growth with less chilling but not normal growth.

Farmer: In eastern Tennessee one must wait until mid-February to get a rapid growth response to forcing with black cherry and northern red oak.

Shreve: I would like to toss into this discussion still another factor:Could this not be simply a matter of photoperiod? For example, we have in our seed orchard in Manhattan, Kansas, an exotic example—English walnut— some from the Carpathian Mountains, some from the Baltic region. These origins freeze simply because their photoperiod responses cause them to pop out too early in the spring. At least that is the impression I have. On the other hand, sources from Italy, the Balkans, and Austria come out very much like out native walnuts, and they don't freeze. It appears that those coming from latitutdes rather close to our own perform quite well. Their respones have suggested to me that photoperiod could have some bearing on results.

Nienstaedt: You are bringing up a tricky relationship. Irgens-Moller, working with Douglas-fir, has, I think, come up with this same relationship. Some of his high-elevation sources did not follow the pattern he had anticipated, and he explained results on the basis of their greater sensitivity to photoperiod. So, I think photoperiod may enter into this; but most studies have indicated that photoperiod has little, if any, effect. Now, again, photoperiod and chilling interact. One can substitute chilling with photoperiod, i.e., with long photoperiod; but just what takes place physiologically I don't believe anybody knows.