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The Role of the Dendrology Course in the Teaching of Genetics*)

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Introduction

Most professional groups have at least two concerns in common, namely to perpetuate themselves by the recruitment of new members, and to have their views accepted by other members of aociety. Forest geneticists are no different. In fact, if these two activities were struck from the repertoire of legitimate professional conduct, some of us would have to look for a new livelihood.

Genetics is a young science — in the context of forestry, even younger — but despite its youth, it has, over the past twenty years, assumed a central position in the domain of biology. Its emerging significance may be attributed to the fact that it has provided both empirical evidence and a theoretical framework, to explain the two most perplexing and seemingly paradoxical phenomena that confront us in all life forms, namely continuity on the one hand, and change on the other. Furthermore, its basic three questions, *i.e.,* what genes are, how they act, and how they are transmitted, are relevant to an understanding of life processes at virtually every level of organization, from the molecule to the population. More importantly, perhaps, while it is a young science, it has addressed itself to such age-old phenomena as the resemblance among parents and progenies, such timeless questions as the origin of species, and such hotly debated, if moot, issues as the nature-vs.-nurture controversy.

Not surprisingly then, the teaching of genetics has become an integral part of any college curriculum in the life sciences. Forestry, among the applied fields, has perhaps, lagged behind in this development for a variety of reasons, some of which may have to do with a certain reluctance many foresters have in accepting a genetic point of view. Instituting special forest-genetics courses has been the most direct effort aimed at a remedy. It is my contention, however, that such specialty courses meet only part of the need, and that other courses may in fact be far more suitable to convey genetic concepts and an appreciation for genetics and evolution to the full spectrum of forestry students. One such course is dendrology.

In this article I will discuss the inherent merits of approaching dendrology in this manner. Hopefully, the article makes some constructive contribution to the perennial debate on curricular reform in forestry education. Furthermore, it may also stimulate discussion among those involved in the increasing number of workshops and short courses aimed at updating practicing foresters in such subjects as genetics, ecology, and silviculture.

Common counter-genetic biases in Forestry

Few of us like to go to the dentist. Memories creep up of some white-coated sadist trying to fragment your jaw with a jackhammer while searching for the last live wire of your central nervous system. Yet, our children seem to be much less reluctant to have their teeth examined. Apparently, the systematic effort by the dental profession to change its image is paying dividends. The modern dentist is your friend in shirtsleeves having an animated chat with you while seemingly getting his work done unbeknown to your novocained nerves, all taking place in a private little art gallery with soft background music.

The analogy may be less frivolous than it seems. Indeed, we may learn from the dentists a trick or two in how make genetics more appealing and how to deliver the ge-

* I dedicate this article to Wolfgang Langner whose writings (Langner, 1958) stimulated my early interest in forest genetics and whose generous hospitality during my 1969–70 visit at Schmalenbeck was much appreciated. The support from the Alexander von Humboldt Foundation is gratefully acknowledged.

netic message more painlessly. To do this, it helps to be aware of some of the more common counter-genetic biases and their sources. Let my try to emphasize those that we regularly encounter in forestry students or perhaps in foresters in general.

A first source is the intrinsically cryptic nature of heredity, particularly in a forestry context. Genes are invisible and so are their ways of influencing the growth and development of trees. This is also true, of course, for other organisms, but what accentuates this cryptic aspect in trees is that the genetic relationships among trees in a stand are generally obscure. Thus, the indirect inferences one can draw to the role of genes from comparing a litter of puppies with the parents, or members of distinct tomato lines with one another, are impossible in the forest. By contrast, the influences of the environment are obvious even to the casual observer: trees are bigger on good sites, suppressed by dominant neighbors, one-sided by the impact of the wind. In fact, the heterogeneous environment in a forest is a direct challenge to the observant forester to detect differenecs between microenvironments and to develop a certain intuition about them.

A second bias, not unique to foresters, is the general feeling that genetic explanations are too mechanistic and simple to satisfactorily explain the continuum of variation in living organisms. The formal either/or propositions commonly associated with classical genetics seem unrealistic, while the more sophisticated treatments of polygenic inheritance seem to be too difficult to visualize. Geneticists are often viewed with suspicion as living in a world of mathematical models only remotely related to real life.

Another reservation about genetics quite typical for foresters stems from the rather distant relationship between trees and *Drosophila* or *Escherichia coli* — yet, those are the organisms at the heart of most genetic discoveries and derivative laws. The extrapolation from a fly, let alone an intestinal bacterium, to a Douglas-fir seems a tall order and, at best, burdened with gross translational errors. To the typical forestry student the genetics he has learned in his introductory biology course is about as relevant to trees as the English he has practiced in a literature class is to writing a technical paper in silviculture. Somewhat related to this view is the feeling that the long life cycle of trees makes manipulations via the genetic route much less efficient in these organisms than those via the environment (in moments of despair, forest geneticists share this view).

A further contributing factor to the counter-genetic bias is the high affinity to a natural environment we so commonly find in foresters. The outdoor mystique is still a major motivating force in the recruitment of forestry students even in an age when most practicioners have become desk-bound and the bulk of field work has been delegated to technicians. The lure of the woods seems to have lost little of its magic in the era of sophisticated technology. Furthermore, the recent ecology movement has given it legitimacy and scientific respectability. In this context, forests are certainly not viewed as uniform monocultures of supertrees — yet, this is precisely the image that forest genetics conjures largely because of its preoccupation with tree improvement. The notion of man, the manipulator, laying his heavy hand on the presumably intricate genetic architecture of the forest, is alarming to many foresters, suspect to most.

A last reservation, perhaps not unrelated to the preceding one, may be grounded in the religious sphere. I am unaware of any statistic documenting a disproportionately high frequency among forestry students of people with strong religious beliefs — yet, personal experience seems to indicate so. In any event, strong objections against concepts of evolution and genetics are repeatedly raised by members of religious groups with fundamentalist leanings.

Some of these biases are more plausible than others, but regardless of their legitimacy, they are real. Furthermore, while anyone of them may be sufficient to hinder the acceptance of genetic facts, several of them often reinforce each other in a given case. The result is the emergence of two opposing groups among foresters, the "disbelievers" as they call themselves, and the "believers" with perhaps an intermediate group of those who acknowledge a genetic dimension but attribute little importance to it. Needless to say, the "disbelievers" will tend to stay away from genetic instruction, particularly where it is offered on an elective basis.

The persistence of genetic illiteracy among foresters should be of more than academic concern to us since it will make itself felt in a variety of ways ranging from ill-conceived forestry practices to poor research, all having some economical, and perhaps worse, biological impact.

Are there effective ways to dispel these biases and, if so, in which way can the dendrology course serve this purpose?

The dendrology course as an opportunity

Dendrology is one of the first forestry courses taken by forestry students. They typically enroll in it after several semesters in the basic sciences when they are eager to get to the object of their future profession, the trees. Yet, traditionally, dendrology has also been one of the dullest courses, emphasizing descriptive, encyclopedic knowledge. In fact, over the years, neophytes have learned to expect from it little more than how to identify trees WIANT, 1968; LANNER, 1969; COUFAL and MARTIN, 1970; FECHNER, 1972). All the more they react favorably to a dynamic approach aimed at an understanding rather than the storage of memorized facts. Evolutionary genetics is eminently suited to provide such a dimension for dendrology and to turn it into a course that also presents a more challenging image of modern forestry, namely that of an integrative field using current information of relevant disciplines.

Dendrology is taken by virtually all forestry students, often even by students from other fields such as landscape architecture, botany, zoology, wildlife biology, outdoor recreation. Thus, it reaches a broad audience — not just the "believers" — and permits recruitment from a large pool. It also allows the student to develop certain expectations about a subsequent forest-genetics course while acquiring a conceptual framework to make it more of a success.

The dendrology course offers a unique opportunity to convey a broader concept of forest genetics than mere tree improvement. Students and practicing foresters alike often view the geneticist as obsessed by the super-tree syndrome and bent on systematically replacing the existing forests by production monocultures. Yet, the legitimate domain of forest genetics encompasses such diverse studies as the genetic architecture of natural populations; genecology; the breeding biology of forest trees; chemotaxonomy and chemical genetics; cytotaxonomy; developmental genetics at the individual tree level; gene conservation and the varied aspects of tree domestication; to name a few. It is easy to weave elements of such studies into the fabric of dendrology, provided one interprets the mission of the course as developing a perspective of trees in a broad sense.

Another opportunity offered by the dendrology course pertains to a largely didactic aspect. In designing a forest-genetics course one is commonly confronted with the dilemma of whether or not to add laboratory and field exercises. Their intrinsic merits are undebatable, but materials and opportunities may be limited and insufficient to justify a lab session. Furthermore, such sessions demand more time and effort from the student, a commitment that may well discourage many from taking the course. Dendrology, on the other hand, is by its very nature laboratory and field oriented and provides, thus, an ideal setting for illustrating genetic concepts and reinforcing them in the students through first-hand observation.

The dendrology course as a legitimate forum for genetics

At the risk of stating the obvious, it is hard to conceive of a modern dendrology course that does not adequately elucidate the continuum of variation in trees and the emergence of species within a genetic/evolutionary framework. In such a context the student is not only permitted but, in fact, expected to observe, discover, and interpret variation at all levels of organization from the array of leaf sizes and shapes within a single tree, to the discrete reproductive features of different families. More importanly, unless a student is "calibrated" early to a stochastic view of nature, he is likely to fall for such simplistic notions as typological species, species prototypes, sterile hybrids, etc., because they are convenient. It will then take another round of education — and many may never experience it — to dispose of such misconcepts. Thus, I disagree with the view that "the first task of a course in dendrology must remain training the student to identify trees" (COUFAL and MARTIN, 1970). I find it much more crucial that we provide the student with a conceptual framework within which he can accommodate the organismal diversity he encounters, and with the necessary tools to make it operational. In such a course the ability to identify species will be a desirable (and practically inevitable) by-product but with no higher priority than the ability to perceive and interpret relevant variation beyond existing classifications.

Similarly, it is hard to discuss the diversity of tree species without considering adaptation, or "adaptive strategies", *i.e.*, adaptations employed to cope with patterns of environmental variability (LEVINS, 1968). A student should learn to think of the most probable selection pressures operative in different environments or at different phases in a life cycle and their possible influence on the various morphological and physiological traits evident in a tree, the correlations of such traits, and the likely costs and benefits for them to be maintained or improved upon. Typically, this reasoning will be elicited from the comparison of allopatric species and will work its way towards the formulation of testable hypotheses aimed at explaining intraspecific variation. For example, recognition of the difference in foliar glaucousness between conifer species along the west coast of North America and related species in the interior, may well lead to the postulate that a similar trend should occur within those species whose range encompasses both regions. If indeed so, as for example in the case of *Abies concolor* (HAMRICK and LIBBY, 1972), the student is then more receptive for the anatomical and physiological explanation of the phenomenon (ZOBEL, 1975). In this manner, observable traits transcend the value of descriptive diagnostics and assume functional meaning. In the absence of such considerations, species diversity is merely an inventory of a myriad of details painful to memorize.

A further case for a genetic approach to dendrology can be made in connection with interspecific hybrids. They abound in trees, yet seem to be singularly unpleasant to classical dendrologists and are only cursorily treated even in the latest editions of traditional textbooks (*e.g.*, HARLOW and HARRAR, 1969). However, to the modern biologist they offer a most intriguing focal point to consider the comparative ecology of sympatric species, the role of hybrid habitats, the operation and breakdown of reproductive isolating mechanisms, the inheritance patterns of groups of traits, as well as the significance of introgression as an opportunity for gene flow. What makes this even more attractive is that there is no shortage of well documented studies of both natural and artificial hybridization in forest trees, providing a rich material for discussion. By contrast, the failure to expose students to concepts of hybridization often reinforces in them a static view of the species and a certain disposition to casually dismiss anything unfamiliar as "some sort of hybrid".

Genetics serves as an excellent bridge to introduce concepts of organic evolution — in fact, one without the other seems as incomplete as a one-legged biped. To discuss the evolution of trees merely in the context of plant geography and paleobotany not only puts the student to sleep but presents a macroevolutionary picture that seems remote from current, observable phenomena and hard to grasp in its time dimension. Greater emphasis on microevolution and the sensitivity of gene frequencies to the mechanisms of mutation, migration, selection, and reproductive sampling errors makes evolution a far more immediate proposition. This, in turn, takes the discussion out of the purely postdictive realm and invites attempts at prediction — a most appropriate exercise for students of dendrology in view of the increasing impact of man on forest and shade trees.

Another argument in favor of a genetic bias is that modern principles of biological classification rest heavily on genetic concepts (*e.g.*, SNEATH and SOKAL, 1973; SOKAL, 1974; SOLBRIG, 1970). Indeed, it is difficult to understand the reliability of an existing classification, or the need for its revision, without recognizing the significance of multiple traits under polygenic control, population variation and its influence on sampling, the relationship of genotype to phenotype, and the role of the experiment in taxonomy. To block dendrology students from this view is to make them into blind practicioners of a branch of science — or art, as some taxonomists have it — in which they could be contributing participants.

Inductive approach

Once a commitment has been made to present dendrology in an evolutionary/genetic context, it is up to the instructor to choose the opportunities, instructional techniques, and materials that serve the purpose and suit the circumstance. Rather than elaborating on the many ways in which this can be done, let me focus on one single aspect I have found to be quite helpful in my attempts at dispelling countergenetic biases in forestry students. It may be described as an inductive approach to learning and emphasizes discovery through intensive student involvement. Three examples of short exercises may serve to illustrate the common denominator.

(a) *Twin Exercise***

Occasional twin seedlings can be found in Douglas-fir. Their genetic correlation ranges from 0.5, in the case of unrelated pollen grains being involved, to 1.0, in the case of cleavage polyembryony (reviewed in ALLEN and OWENS, 1972). Members of a pair typically look very similar, whereas different pairs show various degrees of dissimilarity among each other.

The students are shown 30 two-year-old seedlings randomly arranged, each in an individual container and identifiable by a number. The task is to find 12 pairs of twins among these seedlings and to group them accordingly. The students then begin sorting out the most obvious pairs and gradually proceed to the more cryptic ones, constantly testing a candidate against the residual variation. After completion, an attempt is made at describing the discriminating traits, qualitatively and quantitatively.

The exercise is essentially one of partitioning variation into its "within" and "between" components and can be done with other suitable material such as different clones, provenances, etc. It is important that the plants can be moved around so as to permit different groupings. In this manner, what appears first as a random assortment of variation gradually resolves itself into an orderly array structured according to a genetic organizing principle. Student response never fails and ranges from "wow!" to an expression of amazement that what holds for people seems also to hold for trees.

(b) *Hybrid Exercise*

Most of us are fascinated by hybrids. Intuitively perhaps the most pleasing aspect about them is that they invite and reward comparison with a specific model, *i.e.*, the intermediacy of the hybrid between the parentals. Furthermore, there is something about hybrids that appeals to the creative manipulator in man.

The students are given a plastic bag containing 50 freshly collected leaves. They are told that these leaves come from five different trees, 10 from each, all trees being members of the genus *Populus*. However, whereas four trees are representatives of four different species, the fifth is an interspecific hybrid between two of the others. The task is to find the hybrid and its parentals, assuming the former is intermediate between the latter. Once found, the diagnosis has to be defended by providing all the possible evidence of leaf traits supporting it. Identification of the species and hybrid is immaterial — in fact, the exercise can be successfully conducted with beginning students in the first laboratory session.

The exercise involves a three-phase process: (i) sorting out the leaves into five lots, (ii) arranging the lots according to the ordering principle, and (iii) discovering all traits that support the case. If appropriate material is chosen (in our case, *e.g., Populus tremuloides, P. nigra italica, P. deltoides, P. trichocarpa*, and the F_1 hybrid between the last two), the third phase can be very rewarding since the perceptive student will discover many traits, even texture and smell, contributing to the diagnosis.

(c) *Mutation Exercise*

The image of a white-eyed fruit fly or of an albino germinant is hardly apt to generate an understanding of how mutation provides raw material for natural selection. Many more subtle plant mutants exist, *(e. g.*, the many leaf-shape mutants in tomato) but relatively few well-documented cases are known in forest trees. Thus, it may be more appropriate to approach this topic from another angle, namely to inflict "mutations" and to study their effects. A good material for this purpose is the maple samara.

After an introduction to seed-dispersal mechanisms in general, and to samara flight in particular, (see NORBERG, 1973), the students are given a mass of freshly collected samaras, in our case from the abundant *Acer macrophyllum*. They then experiment with various modifications of the samara, *i.e.*, trimming the wing in a variety of ways, changing its weight or weight distribution by soaking it, or portions of it, in water; dropping it from various suspension angles, etc. For any modification they match the "mutant" with a control, predict the outcome of comparative flight tests, and then test the prediction in 20 trials. Apart from studying the reasons for the particular outcome, they can speculate under which conditions the modification would prove advantageous, under which disadvantageous.

Finally, many different types of samaras are demonstrated from angiosperms to gymnosperms, to show the spectrum of actual changes and to discuss their possible adaptive significance.

Each of the exercises described can be modified in many ways. Even in their simplest form, however, their impact seems to be almost out of proportion to the simplicity of the material and the preparations required, compared to some more sophisticated and elaborate demonstrations. I attribute this to a process which all three seem to facilitate and which we might describe as a progressive involvement of the student at successively higher levels of intensity, each triggered by a positive feedback at the preceding level from an observation made or an insight gained. It is hardly a novel phenomenon — we just might make more use of it in teaching genetics.

What price?

Clearly, the allocation of time and effort to genetic and evolutionary concepts must happen at the expense of material that has traditionally received more attention in dendrology. Can the resulting course still be legitimately called dendrology?

I would argue so. For one thing, we must realize that to a large extent the genetic/evolutionary orientation is a matter of perspective. In other words, once the most basic concepts have been introduced, there are ample opportunities to interweave them with descriptive information on individual taxa under discussion. Thus, the absolute time "sacrificed" is rather modest.

Where does this time come from? Two likely components to be trimmed are the number of species covered and the time spent in describing the remainder. The trimming of the species list is not a trivial matter because we still hope to produce a student who is reasonably proficient in the identification of trees. Furthermore, it takes a "critical mass" of diverse genera and species to effectively convey principles of classification and identification, let alone to develop an appreciation of evolutionary adaptation. Accordingly, the ultimate choice of species to be covered is critical for the success of this approach (to give a specific figure, our students are expected to identify 100 species from 43 genera and 20 families). The reduction in lecture time allocated to species description seems less serious since most dendrology texts provide this information in a well organized manner. Also, the students seem to be much

** This exercise was thought up by B. C. WILSON, Washington State Department of Natural Resources, Olympia, who also had found and provided the material.

more receptive to descriptive details in the field rather than in the classroom.

Finally, I would argue that if good judgment prevails in the choice of taxa and illustrative examples, the added conceptual framework is likely to enhance familiarity with the tree species covered. Thus, while the shift in emphasis cuts down on numbers, it adds a dimension of understanding that is apt to more permanently anchor those particular species in the student's memory. Hopefully, the student emerges from such a course with less encyclopedic but more operational knowledge — a desirable state of affairs if we believe in educating our foresters for tomorrow rather than today.

Conclusions

1. Because of intrinsic and extrinsic factors, the role of genetics in forestry is often poorly appreciated by the professional forester. Formal exposure to the subject in a specialized forest-genetics course is necessary and now a common practice in modern forestry curricula but often limited in scope and audience. Dendrology offers an opportune and legitimate forum for the introduction of genetic and evolutionary concepts.
2. Forest geneticists should be encouraged to involve themselves in dendrology teaching. Those that do may consider it an opportunity rather than a detraction from their role as geneticists. In fact, they may well experience a broadening of their perspective from dealing with a greater variety of tree species, life cycles, and adaptive strategies — a process that may enhance their resourcefulness and flexibility in approaching genetic problems.
3. Graduate students in forest genetics should be given the opportunity to assist in dendrology instruction so as to gain experience and proficiency in this domain.
4. Arboreta, botanical gardens, and other plant collections with an instructional purpose in dendrology should be systematically converted from "tree zoos" to displays reflecting modern concepts of biology. Accordingly, they should have appropriate examples documenting the various levels of intraspecific variation and interspecific hybridization. Special efforts should be made to balance the often atypical ornamental cultivars of a species with more normal specimens from natural populations. Forest geneticists, both in terms of their training and professional experience, are well suited to contribute to this effort.
5. Some of the instructional programs developed for dendrology with an evolutionary/genetic orientation may well prove successful in courses aimed at the updating of professional foresters in genetics, ecology, and silviculture.

Key words: Teaching Forest Genetics, Dendrology, Arboreta, Botanical Gardens.

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Zusammenfassung

Die Bedeutung, welche der Forstgenetik in der Forstwirtschaft beizumessen ist, wird oft von forstlichen Praktikern unterschätzt. Es ist jedoch notwendig und inzwischen allgemeine Praxis geworden, Forstgenetik zu lehren. Geleheit hierzu bietet insbesondere das Lehrfach Dendrologie, welches in Zukunft von Forstgenetikern vertreten werden sollte. Gleichzeitig sollten Arboreta und botanische Gärten in Zukunft mehr Beispiele für die intraspezifische Variation und interspezifische Hybridisation enthalten und zwar in einem ausgeglichenen Verhältnis zwischen atypischen Formen und typischen Vertretern von Arten aus deren natürlichen Vorkommen.

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