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EVOLUTION IN CHANGING ENVIRONMENTS: THE "SYNTHETIC" WORK OF CLAUSEN, KECK, AND HIESEY

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ABSTRACT

The studies of Clausen, Keck, and Hiesey (CKH) have been widely cited as exemplars of ecotypic differentiation in textbooks and in the primary literature. However, the scope of their findings and achievements is significantly greater than this. In this paper we analyze the research program of CKH, highlighting their major findings during the years when the modern synthesis of evolution was taking shape. That synthesis, curiously, drew little from their examples, although their studies at the Carnegie Institution represent conceptual and methodological work that is still relevant. The works of CKH not only embodied the principles of the nascent synthesis, but often provided needed supporting data. Their classic work, especially on Achillea *and* Potentilla, *produced abundant evidence on population differentiation of many quantitative traits and plant phenotypes, as well as demonstrating the now commonly reported distinction between environmental and genetic determination of traits. Their ecological genetic investigations of quantitative traits in plants were in sharp contrast to contemporaneous animal studies on adaptation that focused on discrete polymorphisms—with correspondingly little influence of the environment on phenotypic expression. Of utmost importance was the demonstration by CKH of adaptive differentiation by natural selection and their approaches to understanding the genetic structure of populations.*

CLAUSEN, KECK, AND HIESEY'S 1948 monograph on ecotypic differentiation in *Achillea* has been referred to as "one of the most often cited but least read" works (Lubchenco and Real 1991:718). Their graphic representation of plant height along the transect from Stanford to Timberline has, deservedly, achieved the status of "textbook example." In the course of re-reading their contributions, however, we have discovered that their work ranged far beyond the documentation of ecotypes that they have been credited with for 50 years, and it was remarkably modern in perspective. Given the breadth of topics of current interest that they addressed, we are surprised that their research is so little known.

Investigating issues that extend from cytogenetics to speciation, Clausen, Keck, and Hiesey (CKH) were chiefly interested with evolution in nature and the understanding of adaptation by natural selection. The tremendous project they maintained for more than twenty years still has no peer and many of the evolutionary issues for which they sought evidence—the roles of hybridization and polyploidy, the nature of species, population differentiation, local adaptation and genetic architecture of quantitative traits—remain exciting problems in evolutionary biology.

In this paper, we present a summary of their work on the evolution of plant populations, and identify areas that have received little attention. We discuss their work in both the context of the evolutionary synthesis that was taking place concurrently and for its contemporary significance. We conclude that, in time, scope, and importance, the achievements of Clausen, Keck, and Hiesey easily equal many of the works already in the pantheon of the synthesis, and deserve renewed attention from evolutionary biologists. Although a detailed investigation of the historical/sociological reasons for the neglect of their work is necessary, we will provide some evidence that bears on these issues.

ECOLOGICAL GENETICS IN THE AGE OF EVOLUTION AND TAXONOMY

In the beginning of the 20th century, genetics was separated from the Darwinian theory of evolution during what Huxley (1942) called the eclipse of Darwinism. Those years, however, saw the establishment of the theoretical foundations of population genetics by Fisher, Wright, and Haldane (Provine 1971), which provided a framework for studies on evolution in natural and experimental populations in the 1930s (but see Lewontin 1980). By the 1940s, a tremendous diversity of researchers had undertaken the study of evolution proper (see Mayr and Provine 1980; Antonovics 1987; Sarkar 1992). The "modern" synthesis flowed from this work due to the efforts of a group of prominent researchers in different fields; the number of individuals credited is currently about five—Dobzhansky, Mayr, Simpson, Stebbins, and sometimes Huxley and Rensch (e.g., see Smocovitis 1997; Futuyma 1998).

Ecological genetics, the field into which we can retrospectively place CKH, is in essence the study of evolution in nature, and E B Ford is considered by many to be its first formal practitioner, even though Ford himself suggested an article by Gerould (1921) on *Colias philodice* as the true origin of the discipline (Endler 1986; Real 1994). The intensive study of Sumner (e.g., 1924, 1926) on variation in *Peromyscus* is a clear example, documenting widespread evidence for genetic bases to intraspecific geographic variation. Weldon's studies (1898, 1901/1902) take the origins of laboratory research on evolution back even further.

In tracing the origins of ecological genetics, Ford cited only zoological literature and, admittedly, the majority of early studies were on animals. Ford justified the exclusion of botanical studies:

> [B]otanists have made noteworthy advances in studying cytology and the genetics of adaptation in wild plants, but they have done relatively little in comparison with ecological geneticists in zoology to detect and analyse evolutionary change and the action of stabilizing selection in nature (Ford 1964:ix).

This odd argument appears to remove the study of the genetics of adaptation from ecological genetics.

There was, however, significant botanical research being conducted in ecological genetics during the 1920s, most notably by Göte Turesson (1922; also see Gregor 1930) on geographic variation. Turesson's studies (initiated in 1916) were on what he called *genecology* ("species-ecology"; Turesson 1923), and he also coined the term *ecotype* to designate locally adapted

populations with habitat-based discontinuous morphological and physiological variation.

In a review of genecology, Bennett (1964) suggested that Turesson's work (1922 et seq.) pioneered a synthesis between genetics and evolution, and provided abundant evidence that selection can produce morphologically differentiated and locally adapted populations. This work may have gone unnoticed by the founders of the population genetics revolution due to their interest in purely genetic problems (Bennett 1964), or perhaps due to the overall taxonomic flavor of Turesson's studies. His ecotype concept was "typological," with an emphasis on ecotypes as discrete entities.

Turesson's studies were not the first to expose differences among local populations by changing the environment, but they were the first to adduce evidence that geographic differentiation in plants was genetically based (reviewed in Clausen et al. 1940:394–407). In addition, Turesson was among the first to recognize local populations as the units of evolution, and envisaged the importance of isolation for differentiation among populations of a species in different habitats (ecotypes) and even within habitats. Subsequent botanical work assessed the reality of discontinuous variability among populations: as early as 1930, Gregor's studies with *Plantago* clearly indicated that geographic differentiation could occur even without total isolation and involved not only discrete but also continuous characters. Huxley, in 1938, would coin the term *cline* to indicate differentiation that occurs along a gradient of character variation in which gene flow is not restricted.

The 1930s also saw the launching of two large scale projects, both supported by the Carnegie Institution of Washington, to explicitly study evolution in nature: Dobzhansky's *Genetics of Natural Populations* (*GNP*), working with *Drosophila pseudoobscura*; and Clausen, Keck, and Hiesey's *Experimental Studies on the Nature of Species* (*ESNOS*), working with dozens of plant species, but most notably *Potentilla* and *Achillea*.

THE PRELUDE: CLAUSEN'S STUDIES ON *VIOLA*

Prior to moving to the United States, Jens Christian Clausen (1891–1969) spent ten years working on the Mendelian and cytogenetics of the genus *Viola* in the Department of Genetics of the Royal Agricultural College in Copenhagen. At the time, many fundamental studies on genetics were carried out by European researchers (e.g., Johannsen, Müntzing, Nilsson-Ehle, Teding, Winge). Clausen's work focused mainly on *Viola* section *Melanium*, and he was quite interested in discovering that *V. tricolor* and *V. arvensis* produced fertile hybrids extensively in areas of overlap, despite differences in chromosome number (Clausen 1921, 1922). In each of these species, regional varieties were recognized on the basis of flower color differences, but variation was present for other characteristics as well as habitat. *Viola tricolor*, for example, typically an erect annual herb, had distinctive dune forms that were prostrate and perennial (Clausen 1926, 1951).

Clausen was quite interested in the relationship between widespread geographic variation and the mechanisms of speciation. He performed extensive crosses, both intervarietal and interspecific, to investigate the genetic bases of the phenotypic differences among natural populations and species. He screened phenotypes of nearly 20,000 individuals from 28 different types of crosses, and analyzed 1400 cytological slides. From the crosses, Clausen found that specific differences between *V. tricolor* (n = 13) and *V. arvensis* (n = 17)—such as petal size, lack of labellum, and petal color—are determined by Mendelian genes that can be separated or combined by crossing, although some traits deviated from perfect Mendelian segregation due to genetic linkage. Arising also among the offspring of interspecific crosses were new segregants that were either completely or partially sterile. Crosses of *V. arvensis* and *V. tricolor* gave rise to: (i) a new type, morphologically variable and differing from both parents but with a constant chromosome number of 14; and (ii) a sort of *species novum*, *V. hyperchromatica*, with a higher number of chromosomes (21–23) and differing in many characters from the parental species. Intervarietal crosses within *V. arvensis* resulted in a new fertile type with n = 16 (Clausen 1926).

Despite the ready production of divergent forms, Clausen noted that segregants were competitively inferior to the pure parental types, and deduced that selection operated against hybrids:

[M]ost of the segregated types cannot, even in experimental plots, compete with the pure *arvensis* . . . seedlings of *arvensis* will have sprung up and covered many of the experimental plants, despite the start given to the latter (Clausen 1926:142).

At the time, some workers (most notably Bateson and DeVries) favored a theory of abrupt, mutational speciation over the gradual transformation envisioned by Darwin. Clausen recognized that his data could provide evidence for or against these alternatives. His crossing data and cytological analyses led him to reject mutational speciation for *Viola;* instead he hypothesized speciation following hybridization:

> [B]oth *arvensis* and *tricolor* may be segregation types from some crossing between two other species . . . *V. tricolor* and *arvensis* might then be supposed to have migrated thence and established themselves throughout Europe (Clausen 1926:140).

THE BEGINNINGS AT CARNEGIE

In 1918, F Clements and H M Hall at the Carnegie Institution in Stanford, CA, initiated work on experimental taxonomy. After separating his research program from that of Clements, Hall (1874–1932) began his own series of transplant experiments in California in 1926 (McIntosh 1985) along a transect from the coast to the summit of the Sierra Nevada (Hiesey 1940). By the end of the 1920s, both David D Keck and William M Hiesey were associated with Hall's projects. Three main experimental stations were established: Stanford (30 m above sea level), Mather (1400 m), and Timberline (Slate Creek Valley, 3050 m). The stations differ markedly in climatic conditions and species composition, and Hall recognized this as an ideal scenario to evaluate the effect of the environment on plant phenotypic expression. Hall summarized his goals: "(1) contributions towards a rational and complete classification of the products of organic evolution, and (2) an increase in understanding of the processes operative in the development of these products" (1930:208). Hall believed that information was needed on the composition of species (genetic units, races) and on the causes that promote changes. His group examined as many as 500 species from which they chose several groups specifically suited for their

studies. Unfortunately, Hall's sudden death in March of 1932 created a major barrier for the completion of these studies.

Jens Clausen joined the Carnegie Institution, Division of Plant Biology, in September of 1931 in the field of cytology to create a "valuable link connecting taxonomy and ecology with genetics" (Spoehr 1932:12). Following Hall's death in 1932, Clausen took over the experiments at the field stations.

LAUNCHING A LIFE PROJECT

At the Sixth International Congress of Genetics in Ithaca, NY (where S Wright delivered an abstract of his famous paper "Evolution in Mendelian Populations"), Clausen presented an outline of the work he felt necessary for an understanding of evolution:

> As long as genetics is concerned with the individual genes only, it makes no difference which type of material is utilized. But genetics of our days is going further, trying to apply its findings toward a revision of our conception of living organisms, their diversity and mutual relation as well as the origin of this diversity. This demands a closer contact with the living organisms in natural surroundings (Clausen 1932:21).

For this, he proposed the integrated study of several objectives with a clear focus on microevolution, adaptation, and speciation:

> First, the extensive field study of variation within limited groups of species is necessary . . . Next, it must be determined by various means which part of this variation is inherited and which one is only of modificatory nature. Further, a cytological study of the variation is indispensable, covering taxonomic units of smaller as well as of larger order and covering types from all subdivisions of the area inhabited by the group of species subject to investigation . . . The next step is an analysis of the genetical differences underlying the taxonomic differences as far as this is feasible. This involves crossings between natural varieties, subspecies and species, and in some cases even genera. A study of different degrees of intersterility or incompatibility is important because these phenomena give us a clue to the understanding of the way species become separated from each other . . . Another problem is why the various units are where they are

in nature. A study of this problem may, ultimately, become a study of the physiological effect of genes . . . The final goal of the type of research here outlined . . . should attempt to trace the lines along which the present day species have developed and, wherever possible, substantiate these studies by synthetic methods (Clausen 1932:21–23).

We note that the proposed program was comparable in scope and initiated prior to Dobzhansky's *Genetics of Natural Populations*, considered the most important body of work in evolutionary biology (Lewontin et al. 1981). For his research on the GNP, Dobzhansky received financial support from the Carnegie Institution from 1937–1950. The first paper of the *GNP* series appeared in 1938, although earlier papers published with Sturtevant can be considered as the inauguration (Provine 1981). Unlike the work of CKH, the importance and impact of Dobzhansky's work for the study of evolution and the evolutionary synthesis is universally recognized.

The studies of CKH, including the four volumes of *ESNOS*, a book by Clausen, and various journal articles, are witness to the achievement of the goals outlined in 1931. These dealt with numerous species, many polygenic characters, adaptation, natural selection, phenotypic plasticity, development, and genetic structure of populations. These remain research issues of significant interest in modern evolutionary biology.

EXPERIMENTAL TAXONOMY, SPECIES CONCEPTS, AND SPECIATION

Following Hall's death, Clausen, with Keck and Hiesey, quickly organized the available data and identified aspects of interest to pursue. In their first report, while maintaining the objectives of Hall, they emphasized:

> [T]hat the complete picture of evolutionary processes could only be obtained through the pooling of these [Hall's] data with those from related fields, especially cytology and genetics . . . This may be called a joint study of the products of organic evolution as they occur under natural conditions . . . All this should lead to and form the proper background for a study in experimental evolution and phylogeny of certain groups of plants (Clausen et al. 1932:201).

Thus, while maintaining an interest in taxonomy, they placed increased emphasis on evolutionary processes. Hiesey summarized data taken from previous years (Clausen et al. 1933), and species to be utilized for continued data collection were identified. The project gained momentum, with rapid advances described in the yearly reports (Clausen et al. 1933–38). For example, in 1934 they reported a new series of transplants to the three stations, a survey of California species of *Madia* and *Hemizonia*, the establishment of 500 cultures of 70 species of the Madiinae, and crosses and cytological studies (Clausen et al. 1934).

Working with intra and interspecific variation made it necessary for them to deal with the issues that surround the definition of a species, and they were strong advocates of a multidisciplinary approach to the problem:

> One of the most vexing problems to modern biologists is the species problem, and the experiments were designed to yield positive or negative answers on it. The answers from field data, chromosome investigations, and some 40 hybridization experiments in the genus *Layia* are so convincing and clarifying that this genus appears to be a perfect class-room example for the purpose and is to be used as an illustration in a forthcoming paper on the species question (Clausen et al. 1935:205).

For CKH, these investigations of the *Layia* group (see Figure 1) provided clear evidence of the reality of species in nature, and formed a foundation for their views on speciation (Clausen et al. 1941, 1947; Clausen 1951). The *Layia* work was further solidified by generalizations derived from their extensive investigations of a taxonomically diverse group of species (Clausen et al. 1935:201–202).

Although the "forthcoming paper" did not appear in a refereed journal until 1939, it is clear as early as 1936 that CKH were developing a "biological" view of plant species, a view derived in part from their unique research program to discover the mechanisms of isolation. The form of their species concept was quite similar to those proposed by Dobzhansky and Mayr:

> Species are separated by genetic barriers of various degree and effect. Their hybrids are
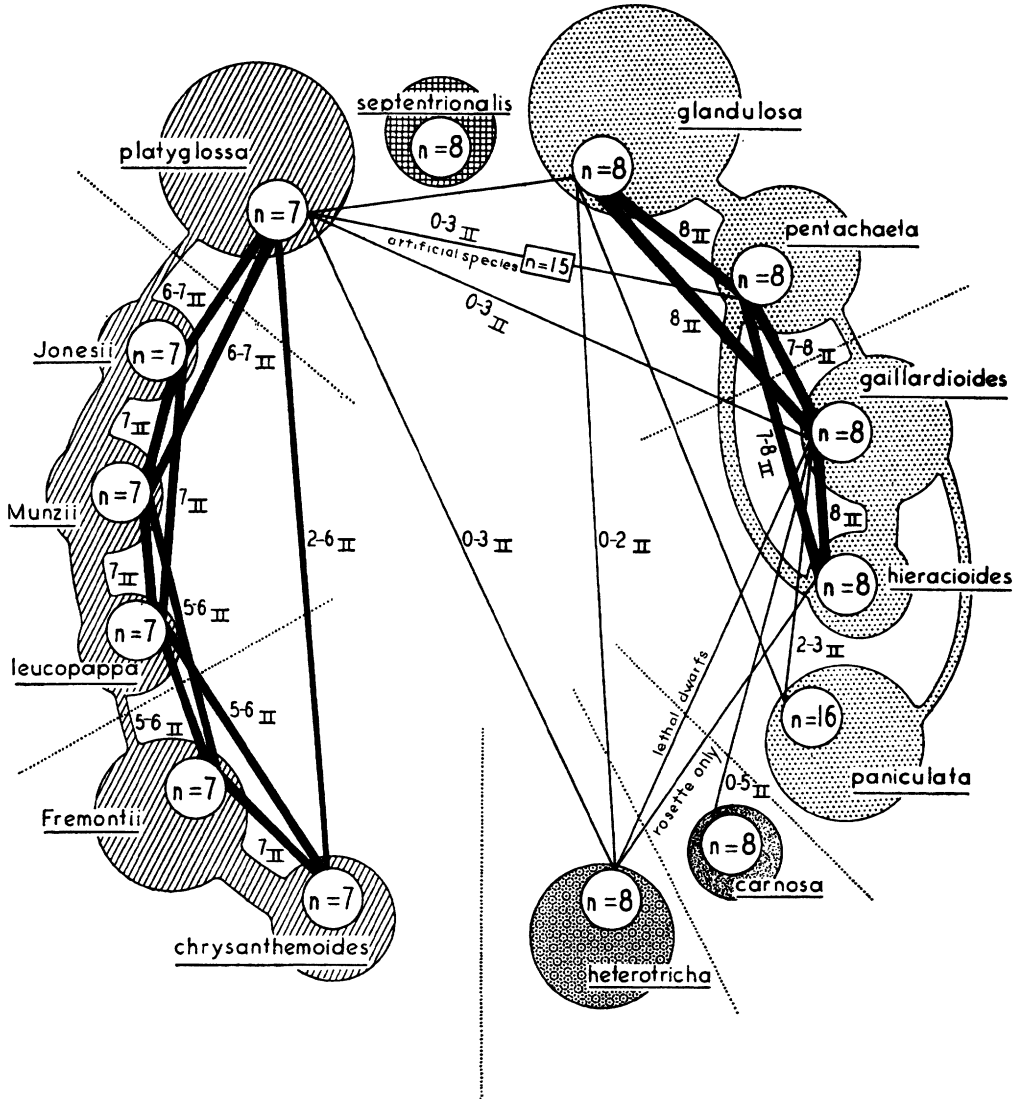
FIGURE 1.

Depiction of the relationships within the genus *Layia* based on barriers to crossing. Shaded circles indicate species, with haploid chromosome numbers indicated. Species within the same shading are considered to be more closely related, and dotted lines represent major morphological discontinuities among groups. The width of continuous lines indicates the degree of successful intercrossing between a given pair of species; in most cases the highest fertility was only 50%. Unsuccessful crosses are not shown. (From Clausen et al. 1941.)

either partially or completely sterile, or, if fertile, most of the second generation shows a remarkable lack of vigor and would be eliminated under natural conditions (Clausen et al. 1936:209).

In 1937, Dobzhansky would define a species as "that stage of evolutionary process, 'at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding'" (Dobzhansky 1937: 312). Dobzhansky's influence can be seen in CKH's more formal species concept:

> [P]lants are organized into groups, the members of each of which are able to interchange their genes freely in all proportions without detriment to the offspring. Such groups are separated from one another by internal barriers that are of a genetic-physiologic nature (including chromosomal barriers) that prevent such free interchange (Clausen et al. 1939:104).

Mayr, in his 1942 book, criticized Dobzhansky's definition: "A species is not a stage of a process, but the result of a process . . . Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942:119–120). Mayr, however, in the section "The Plant Species" (p 122), did not mention CKH's definition.

Increased study of plant hybridization in previous decades had not only revealed it to be not rare, but also demonstrated that hybrids between species may be fertile, leading some plant taxonomists to consider species as abstractions (discussed in Clausen et al. 1939). CKH's response was to exhaustively examine the effects of hybridization experimentally, attempting about 400 hybrid combinations (involving 70 species in six genera of Madiinae). They found that more than 200 of these crosses were initially successful. However, in subsequent generations "only a small percentage of the genic recombinations survive . . . [and] vigor of the survivors is reduced, so that only few members of the second generation are fit for the severe competition in nature" (Clausen et al. 1939:103). They concluded that the production of interspecific hybrids does not necessarily imply that species do not exist as natural units.

EXPERIMENTAL STUDIES ON THE NATURE OF SPECIES — *ESNOS*

ESNOS I

The first formal publication containing the results of the experimental data collected mainly from 1934–1937 appeared in 1940 as a 452 page book published by the Carnegie Institution entitled *Experimental Studies on the Nature of Species. I. Effect of varied environments on western North American plants.* Of 182 species studied, 59 provided data included in the report. A large part of each section of the book is devoted to information on phenotypic variation at the transplant sites, both within and among populations of a species, and depictions of reaction norms (their "reaction patterns": the average phenotypic expression of a clone or population at the three different elevations). Moreover, cytological studies were often added. Taxonomic issues were frequently discussed (e.g., *Potentilla glandulosa, Penstemon,* and *Zauschneria*), and in some instances, inbreeding depression and cross compatibility among "units" (races, subspecies, species).

CKH unmistakably recognized that the kinds of evidence they were gathering were important in relation to adaptation and evolution of natural populations:

> Perhaps one of the most valuable results of the transplant work is the pointing out of the wealth of unsolved problems pertaining to the relation between plant characteristics and environment. This is especially evident in the case of species having natural races distributed at low, high, and intermediate elevations . . . Fundamental problems are thus suggested in the study of the anatomical and physiological differences between races in the same or in closely related species with the possibility of obtaining evidence on the interrelationships between plant structure and physiology on the one hand and natural selection and survival on the other (Clausen et al. 1935:203).

The major conclusions of *ESNOS I* were simple, concise, and persuasive. (1) Species can be composed of multiple differentiated populations; those species with wide distributions tend to have more differentiated races; and higher differentiation may be expected in heterogeneous habitats. (2) Despite extensive phenotypic plasticity, ecotypic differentiation is not

due to plasticity alone. (3) Adaptation favoring local survival and reproduction promotes population differentiation, and thus ranges of environmental tolerance will vary for each population.

Phenotypic Variation

The transplant design made it clear that plant phenotypic variability was the result of an interplay between genetic differences and the environment (Clausen et al. 1940). Genotypes from each population retained genetic distinctiveness, even though many characters were environmentally modifiable (plastic). Other characters were shown to be heritable but nonplastic, including many related to architecture and form. Plastic responses could be rapidly induced, and the extent of plasticity varied among species, populations, and genotypes within population—a striking example of crossing reaction norms was found among ecotypes of *Zauschneria* grown at Stanford and Mather (Clausen et al. 1940:Figure 88).

One plastic trait CKH found noteworthy was anthocyanin development in *P. glandulosa*. They found that *P. glandulosa* subspecies *reflexa* (from the foothills) developed anthocyanin in its herbaceous parts in all three environments, with pigmentation most intense at Timberline. Subspecies *nevadensis* (from high altitudes) developed coloration in stems, petioles, and leaf veins at Timberline, but almost no coloration at Mather and Stanford. Their conclusions noted both the overall subspecific differences, the environmental effects, and the differences in response between the subspecies. These results led them to hypothesize about a relationship between pigmentation and resistance to cold conditions.

Genetic Bases for Differentiation and Adaptation

Observations that higher ploidy levels were more common in unfavorable habitats suggested to some botanists of the time that higher ploidy per se had adaptive significance. Many of the species groups studied by CKH along the transect did show changes in chromosome number (cf. Figure 155 in Clausen et al. 1940). However, although they noted a high percentage of polyploidy in the Sierran transect perennials (and anticipated its relevance in plant evolution (p 425); see Stebbins 1950), CKH

observed no overall correlation between chromosome number and altitude among their taxa. Their results, and a careful examination of recent data from the literature, led them to reject any intrinsic adaptive value to polyploidy. Instead they argued that adaptation to particular environments, and the attendant morphological and physiological differentiation along the transect, was derived from the action of individual genes (p 423–424).

Crossing experiments, particularly in *Potentilla glandulosa*, provided the evidence for allelic differences among races. CKH crossed *Potentilla glandulosa* subspecies *reflexa* (a foothill population) and ssp. *nevadensis* (a subalpine population) and recorded fourteen morphological and physiological characters that distinguish the two. The polygenic nature of most traits was clear: F_1 progeny were generally intermediate between the parents at each individual station, and, in the F_2, recombination of many of the traits was noted. They also noted patterns of genetic linkage specific to each parental population; for example, the coupling of a morphological (petal color) and a physiological trait (earliness of flowering) suggested to them a means for maintaining ecotypic differences even at points of contact.

Inspection of the reaction norms, however, revealed a number of curious patterns of what we now call genotype by environment interaction, and enhanced their insights about the nature of gene expression. F_1 hybrids between ssp. *reflexa* and *nevadensis* displayed intermediate phenotypes for height at Stanford and Mather, but were shorter than both parents at Timberline (i.e., a case of transgressive segregation—trait values beyond the range of the parental phenotypes). F_1 clones had delayed onset of flowering in relation to both parents in Stanford but were intermediate at Mather and Timberline (Figure 2). This observation was a particular puzzle: "As yet we have no satisfactory explanation for this phenomenon, except that it tells us that the interreactions of the factors that determine the time of flowering of a plant in a certain environment are very complex indeed" (Clausen et al. 1940:120). CKH hypothesized that, at Stanford, there might be interference between genes that accelerate growth and genes that determine dormancy.
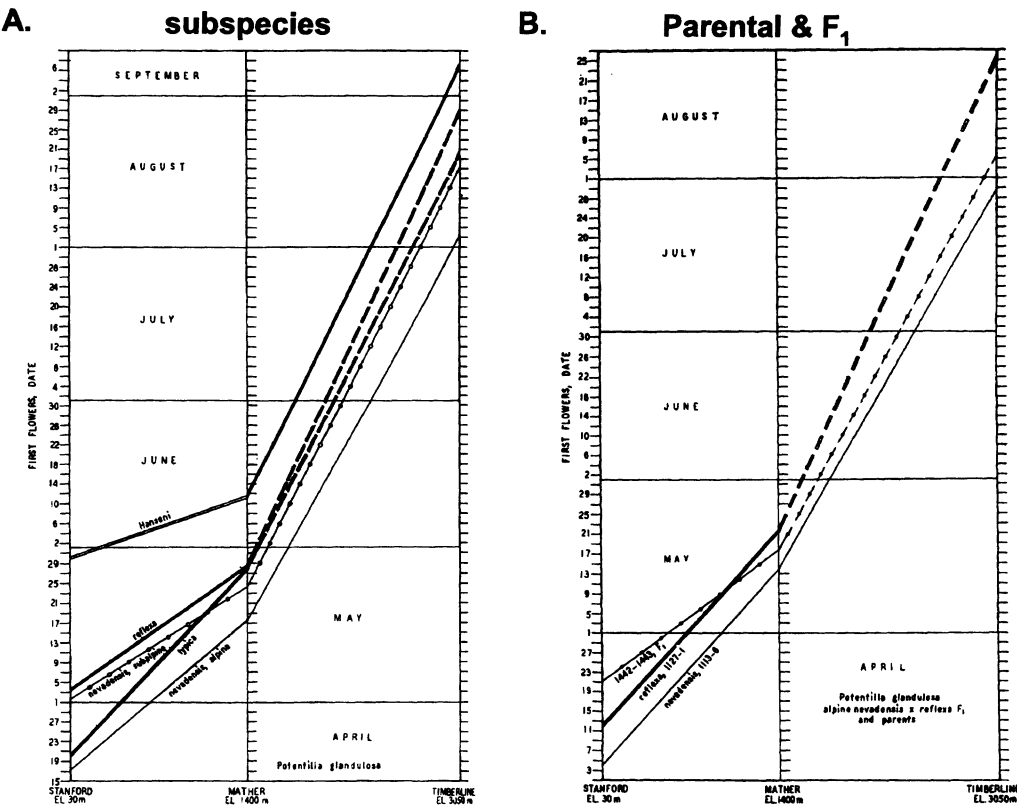
A.   subspecies   **B.   Parental & F₁**

FIGURE 2.

Date of flowering of clones of *Potentilla* grown at three transplant sites in California. **A)** Reaction norms for four subspecies of *P. glandulosa*. **B)** Reaction norms for parental and F₁ plants of a cross between subspecies *reflexa* and *nevadensis*. (Modified from Figures 36 and 45 of Clausen et al. 1940.)

The reaction patterns were also crucial to their interpretations of adaptation. Clones derived from the two populations differed distinctly in survival: at Timberline, the foothill parents survived poorly and all ultimately died, and the F₁ clones (phenotypically more similar to the foothill plants) survived only a few years; Timberline parents survived indefinitely. CKH interpreted this as clear evidence for natural selection. They noted that, despite the enormous potential possible combinations of genes and corresponding phenotypes, only a limited number of differentiated populations were present in nature. This also supported a view that natural selection could produce differentiation in morphological and physiological characters without necessarily creating breeding barriers.

Conclusions

This body of evidence regarding physiological and morphological responses of plants to the environment, the genetic nature of the differences for these characters, and the inferred effects of selection shaped their views on adaptive evolution:

Not only must a plant be in equilibrium with its environment in order to succeed, but its entire gene activity must be in balance . . . Each ecospecies represents a different equilibrium . . . In view of these exacting requirements, it is understandable that evolution is a slow process . . . The very nature of the double demands of internal balance and fitness to the environment is evidently the most important cause of the apparent discontinuity in nature (Clausen et al. 1940:426–427).

This Wrightian view mirrored two current te-
nets of the evolutionary synthesis, namely grad-
ual evolution mediated by natural selection
and gene flow opposing selection; CKH were
among the first and few with evidence. Although
changes in chromosome number might pro-
vide reproductive isolation among populations,
most speciation seemed to be a secondary prod-
uct of local adaptation and differentiation.
This appreciation that evolution could pro-
ceed at a gradual pace was in marked contrast
to other researchers, whose focus on finding
marked differences, particularly in chromo-
some numbers, and lack of interest in the pro-
cess of adaptation made speciation and evolu-
tion seem like very rapid processes.

Their observations on patterns of character
recombination and linkage provided the stim-
ulus for the continuing studies on F_2 progeny
that would be reported in ESNOS IV. Specifi-
cally, they noted that further study at all three
stations would be important to "determine
whether adaptation can be produced by genic
reassortment and selection, and . . . results in
types morphologically similar to the natives"
(p 124).

ESNOS II

The second volume of ESNOS (174 pages)
went to press at the end of 1943 and appeared
in February of 1945. More focused in its subject
matter, it aimed at uncovering the importance of
rapid speciation via polyploidy in plants (through
autopolyploidy, the addition of sets of chro-
mosomes of the same species, or allopoly-
ploidy, chromosomes from a different species).

They studied species of the subtribe Madii-
nae of the Asteraceae, distributed in Mediter-
ranean climates of North and South America.
Of the almost ninety species in eleven genera,
only six polyploids were known in the wild.
Eighty species showed chromosome numbers
from 4 to 14, with 16 and 24 for tetraploids and
hexaploids, respectively. Special attention was
given to the genera Madia (n = 6–9, 14, 16, 24)
and Layia (n = 7, 8, 16; cf. Figure 1). Crosses
between species with different chromosome
numbers allowed CKH to determine the pres-
ence of isolation barriers within Madia and
Layia.

Of the six polyploid species found in nature,
two were hexaploid (both Madia, n = 24) and

four were tetraploid (n = 16; three Madia, one
Layia), and all appeared to have originated
through allopolyploidy via gametic doubling
(unreduced). One hexaploid Madia species
falls within the range of Madia gracilis (n =
16) and Madia citriodora (n = 8), which CKH
implicated as parents through morphological
and cytological analyses. Moreover, CKH pro-
duced this hexaploid experimentally by cross-
ing these species: F_1 plants had n = 24 and
were phenotypically similar to the natural
hexaploid. Although the parent species were
self-fertile, F_1 plants showed very low self-fertil-
ity. However, almost 80% of the resulting F_2
plants were full allopolyploids (2n = 48).

Two other hexaploids synthesized from in-
terspecific crosses did not occur naturally.
Madia nutrammii (2n = 17) was synthesized by
crossing the geographically isolated species
M. nutans (n = 9) and M. rammii (n = 8). F_2
plants were self-fertile and stable (up to five
generations). This "synthesized" species, un-
known in nature, was unable to survive at
Mather, but grew well at Stanford. Experimen-
tal crosses between Layia pentachaeta (n = 8)
and L. platyglossa (n = 7) produced the allo-
polyploid L. pentaglossa (n = 15), but subse-
quent generations were largely sterile with
variable chromosome complements. Exten-
sive field work located only one site with both
species—a single L. pentachaeta in a population
of L. platyglossa. Only three seedlings could be
produced from seed collected from the L. pen-
tachaeta plant—two were hybrids, but neither
subsequently set viable seed.

Following their experimental work, and a
careful review of the literature on polyploids,
CKH attempted some generalizations regard-
ing the conditions favoring the origin of spe-
cies through allopolyploidy, as well as the eco-
logical characteristics of such species.

1) Allopolyploidy plays an important role in
the evolution of higher plants. Genomes
of parental species need to interact in a
harmonious way to produce viable prog-
eny, and crosses between related species
are more likely to be successful; crosses of
species with different chromosome num-
bers leads to nonpairing and reduced re-
combination.

2) Chromosome doubling via production of
unreduced gametes should be a common

mode for the origin of allopolyploids. The establishment of a fertile allopolyploid may take more than two generations.

3) Autopolyploids may be morphologically quite similar to a parental species and occur in mixed or adjacent habitats. In contrast, allopolyploids may occur in different ecological conditions in relation to the parental species, and are not commonly found in intermediate conditions. If characteristics of both parental species segregate in an allopolyploid, strong selection is expected in that habitat.

4) There are two major ways in which species arise. (i) In early stages of plant evolution, ecological differentiation results from selection on genes that confer local adaptation and barriers to interbreeding among populations are weak. Because barriers have a complex genetic basis, their production and thus the process of speciation is expected to be gradual. (ii) Speciation by polyploidy via the addition of genomes (not merely changes in genes) and the attainment of reproductive isolation in relation to the parental species is rapid.

ESNOS III

The third volume (*Environmental responses of climatic races of Achillea*, 129 pages) appeared in 1948; it reported the comprehensive analyses of the responses of different forms of *Achillea* to varying environments. The *A. millefolium* "complex" comprises several species and ecotypes, and was an ideal subject for research due to its wide distribution across varying environmental conditions, ranging from the coast and coast ranges, across the San Joaquin Valley to the foothills, meadows, and timberline in the Sierra Nevada, and into the Great Basin Plateau.

Seeds were collected, germinated, and grown (up to 60 individuals/population) in a common garden at Stanford for 81 natural populations of *Achillea* from western North America, Scandinavia (3), and the Aleutian Islands (6). Populations were characterized (growth, reproduction) and 30 individuals from 14 selected populations were cloned and used for transplanting at the Stanford, Mather, and Timberline field stations. Once each individual plant was cloned, replicates were transplanted to each station and morphological and physiological characters were recorded (e.g., height, number of stems, time of flowering, and survival, among others) over a three year period. Their classic, often reproduced Figure 1 (cf. Stebbins 1950) characterizes the variation in height for various populations of *Achillea* growing at Stanford *prior* to the transplant experiment.

The results of the transplant experiment revealed, as expected, variability in morphological and physiological characters among populations. Survival and reproduction were markedly reduced for some transplanted populations. In contrast, natives did very well in their own environment, supporting their conclusion of local adaptation by selection (Figure 3). CKH differentiated a total of eleven climatic races or ecotypes of *Achillea* along the 200-mile transect across central California. There was genetic differentiation in morphology, and especially for physiological traits, although the selective importance of many characters could not be guessed at. Figure 3 illustrates the evidence of strong selection (i.e., stem lengths of 0 at Timberline), as well as the environment-dependent expression of phenotypic variation among populations, with substantially more differentiation evident at Stanford.

To assess the factors that interact with the genotypes in the field and produce the diversity of reaction norms, CKH performed controlled experiments in which they varied light and day/night temperature. Generally, populations from the coast to Mather performed better in cool days (17°C) and mild nights (13°C) and, in contrast, populations from high altitude and from the Great Basin performed better in warm days (26°C) and nights (17°C). These differences in growth optima reflect the climatic differences between the habitats of the populations: the coastal growing season occurs in winter and spring (December to July), while in the Sierras and Great Basin it is in summer (August). These greenhouse experiments reinforced the important role of climatic factors in shaping physiological characters important in plant survival and reproduction, such as the presence and length of the dormant period, growth rate, onset of flowering, and frost resistance.

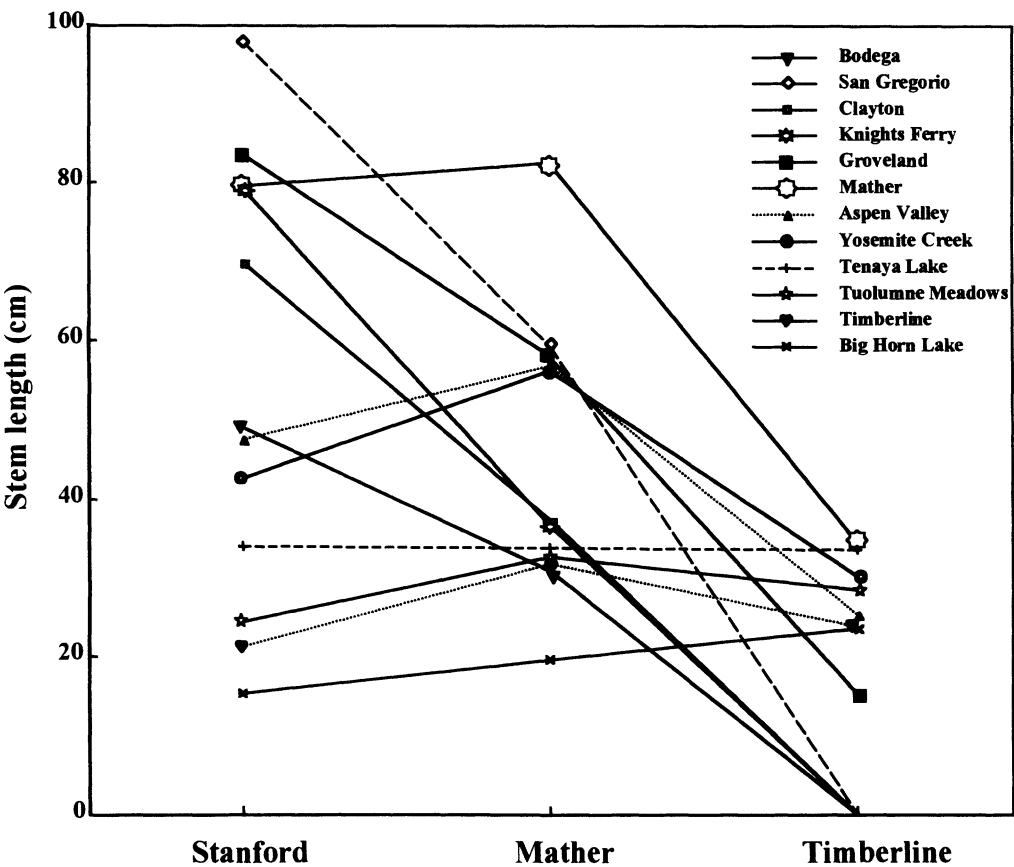This study provided strong support for their

FIGURE 3.

Reaction norms for stem length (the longest stem) of clones of various different populations of *Achillea* (*borealis* and *lanulosa*) at the three transplant stations along a transect from the coast to the Sierra Nevada in Central California (data from Table 19 of Clausen et al. 1948). Some clones did not survive at Timberline.

previous results (Clausen et al. 1940, 1941, 1947) regarding the role of natural selection in the face of gene flow:

> The local populations occur sufficiently close together to permit easy intermixture through dispersal of pollen and seed. The differences found between populations should therefore be due primarily to natural selection rather than to spatial isolation (Clausen et al. 1948:103).

Moreover, this study offered evidence on the adaptive importance of plasticity:

> Some individuals within the race are better fitted than others, but each one has a physiological tolerance that enables it to survive over a range of conditions, and thus meet changes that may occur in its surroundings (p 122).

Further work by Hiesey (1953) would amplify the theme of physiological tolerance: he found extensive within-population variability for *Achillea* grown in controlled environments with different temperatures and daylengths.

ESNOS IV AND NATURAL SELECTION

The fourth volume of *ESNOS*, *Genetic structure of ecological races* by Clausen and Hiesey, went to press in 1956 and was published in 1958; Keck had taken the position of Assistant Director of the New York Botanical Garden.
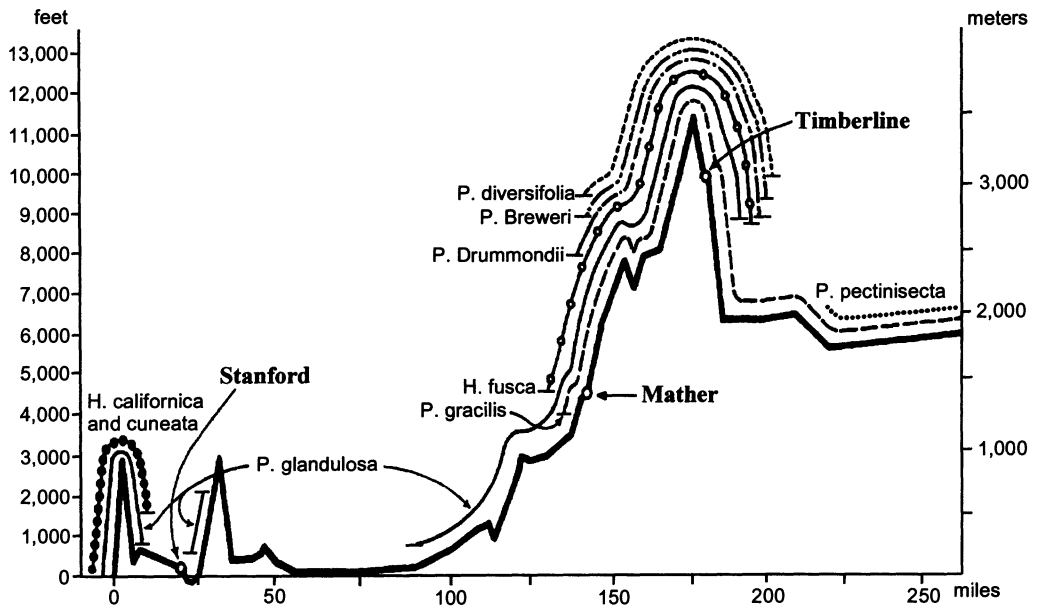
FIGURE 4.

  Altitudinal distribution of the different species of *Potentilla* and *Horkelia* (Rosaceae) along the transect from the coast to the Sierra Nevada in Central California. The three transplant locations (Stanford, Mather, and Timberline) are also shown. (Modified from Figure 154 of Clausen et al. 1940.)

This is a book on ecological genetics and constitutes an extensive study of the genetics of natural populations of *Potentilla glandulosa*. Of particular interest is their analysis of character correlation and plasticity across environments. In addition, *ESNOS IV* contains an extensive review (106 pages) of the knowledge of genetic systems that control adaptive physiological and morphological characters in wild species, and their interaction with the environment.

  Perhaps the greatest of all their achievements in this volume, however, was to tackle the study of natural selection in the wild. Results of the previous transplant experiments led them to focus on the genetics of plant adaptation and natural selection (cf. *ESNOS I*). They chose *Potentilla glandulosa*, with its four subspecies (*typica, reflexa, hansenii,* and *nevadensis*; all n = 7), continuous distribution along the gradient from the coast to the Sierra Nevada (except for the San Joaquin Valley; Figure 4), and no reproductive barriers among subspecies.

  As early as 1934 they had developed an F_2 population of *P. glandulosa*, derived from the

self-pollination of F_1 plants from crosses between foothill (Oak Grove, 760 m altitude; ssp. *reflexa*) and alpine (Timberline, 3050 m altitude; ssp. *nevadensis*) ecotypes (Clausen et al. 1940:114–116). This population formed the basis for their study of natural selection in the wild:

  > Because the F_2 population represents an interchange of genes of two very different climatic ecotypes, and includes segregants representing both parents as well as a host of recombinations, this experiment should test the theory of adaptive evolution by genetic recombination and selection (Clausen et al. 1938:222).

  The foothills population (*reflexa*) is self-compatible and possesses small flowers, and the alpine population (*nevadensis*) is self-incompatible with large flowers, but the subspecies differ in many other morphological and physiological characters (Clausen and Hiesey 1958: Figure 14). Because the foothills population did not survive at Timberline, CKH made crosses between populations and transplanted

F_1 plants to each of the three stations and found that some F_1 plants survived at Timberline (see *ESNOS I*). F_2 plants, obtained by selfing F_1 plants, were grown first in a garden at Stanford, and after first flowering (the second year of growth) each of 578 plants was cloned to get three copies (ramets). One ramet of each clone was transplanted to Stanford (30 m), Mather (1400 m), and Timberline (3050 m) in 1938. Although other crosses were performed, the *nevadensis reflexa* F_2 progeny was the most interesting because it was grown at all three altitudes. Twelve to 19 characters were recorded for each individual from 1938 to 1943. F_3 plants were obtained by selfing selected F_2 plants in 1940, and grown only at Stanford. F_3 plants were measured for four years (1942–1945) to verify the genetic nature of trait differences and estimate the number of genes involved.

Genes Contributing to Character Expression

To estimate the number of genes that control the phenotypic expression of characters, CKH used the array of phenotypes segregating in the F_2 progenies of Oak Grove × Timberline, and from a cross of populations from Santa Barbara (altitude 50 m; ssp. *typica*) and Upper Monarch Lake (3240 m; ssp. *nevadensis*) (Clausen et al. 1940:114). This latter F_2 was grown only at Stanford with a larger sample size. The range of F_2 phenotypes again demonstrated character recombination. In support of their estimation of the number of genes involved, they measured both parental and F_1 phenotypes, and carefully observed how repeatable a trait was within an individual, and how it varied among stations and across years.

Assuming diploidy and gene effects that were polygenic, equal, and additive, they calculated the expected frequencies of phenotypes and their putative genotypes using the binomial approximation when 1, 2, 3 or more genes are segregating. 575 and 961 individuals were scored for the F_2 and more than 2000 for the F_3. Their results suggested that, for the expression of the 19 characters measured, a total of more than 100 genes were involved in the differentiated populations of *Potentilla glandulosa* (Table 1). Most gene effects appeared additive, but evidence of epistasis was present for some traits. Thus, not only did they verify genetic differentiation, but they also estimated

the number of genes involved in the differentiation of locally adapted populations. Clearly, the elucidation of genetic structure was not impossible for natural populations.

Furthermore, changes in phenotypic expression of the same genotypes at the three stations suggested that different sets of genes may be involved in the expression of some characters. For example, for earliness of flowering, substantial transgressive segregation was noted for the F_2 individuals, but the direction of transgression was towards later flowering plants at Mather and earlier flowering plants at Timberline. Clones that were early at one station might be early, intermediate, or late at others.

Of particular interest is their analysis of life-history traits, such as the presence of winter dormancy, earliness of flowering, or physiological characters like frost resistance and the presence of anthocyanin in stems and leaves, for which adaptive roles had been hypothesized earlier (see Clausen et al. 1940). Their analysis of phenotypic variability in the F_2 and F_3 progenies indicated to them that: (1) much more variability was present in natural populations than is typically expressed, and (2) the relations among genes, and between genes and the environment, are complex. For instance, for stem length, controlled by an estimated 20 genes, Clausen and Hiesey found a tremendous diversity of reaction norms among the F_2 clones transplanted to the three stations (Figure 5). Again, phenotypic variation in the F_2 surpassed the range of variability of the parents (transgression). Also, since the estimation of the number of genes that control the expression of a character is based on the observed phenotypic frequencies, different estimates of gene numbers would be obtained for different environments. Although phenotypic variation is high in the three environments, it is lower at Timberline, suggesting limits to plastic responses. Finally, several "canalized" (i.e., nonplastic) genotypes were present among the F_2 plants, although such forms had not been observed in previous work (cf. Clausen et al. 1940).

Natural Selection in the Wild

By exposing the genotypic variability represented by the F_2 genotypes to three environments, and knowing the characteristics that

TABLE 1

Estimated minimum number of genes involved in the inheritance of characters in Potentilla glandulosa
(modified from Clausen and Hiesey 1958)

Traits	Gene Number	Notes
MORPHOLOGICAL/ARCHITECTURAL		
Stem length	~10–20	Many patterns of expression in different environments
Leaf length	~10–20	Environmentally sensitive expression; different sets of genes activated?
Crown height	~3	
Angle of branching	~2	
Density of inflorescence	~1	
Leaflet number in bracts	~1	
REPRODUCTIVE		
Orientation of petals	3	
Petal notch	3	
Petal color	5	Environmentally sensitive expression
Petal width	6	
Petal length	~4	
Sepal length	~5	
Achene weight	~6	
Achene color	4	
PHYSIOLOGICAL/LIFE HISTORY		
Glandular pubescence	5	
Anthocyanin	5	Environmentally sensitive expression
Winter dormancy	3	
Frost susceptibility	~4	
Earliness of flowering	Many	Environmentally sensitive expression; different sets of genes activated?

differentiated the *P. glandulosa* foothills and alpine populations, Clausen and Hiesey expected to find that differences had been shaped by selection, a "repetition" of the evolutionary process. Discerning the effects of selection would be difficult, however, because of the number of genes involved, the extent of phenotypic variation, the environmental effects on trait expression, and character correlations. They tried several different approaches: (1) examination of survival at the three stations; (2) analysis of genetic correlation among characters and their change across stations; (3) calculation of the number of observed and possible reaction norms; and (4) "artificial" selection to find genotypes suited for a diversity of conditions. We describe here the first two approaches (a full description and reanalysis of the various approaches has recently been submitted by Núñez-Farfán and Schlichting).

Survival

For each F_2 plant, they constructed an index value (IV) which summarized the measurements for a variety of characters. Lower in-

dexes indicated phenotypic similarity to the alpine parent (with $IV = 19$), and higher values indicated similarity to the foothill parent ($IV = 53$). The F_1 were intermediate (33–40) and values for the F_2 ranged from 20–48. They divided the different clones into three classes based on IV (20–29, 30–39, 40–49), and contrasted the survival of each class of plants at the three stations for 5–9 years. If clone survival were random, equal proportions of survivors with different *IVs* should be found at each station. The results indicated that at Timberline, clones with lower *IVs* (resembling the alpine parent) had the highest survival (Figure 6), while the clones with intermediate and high *IVs* had low survival. Conversely, survival of clones with low *IV* was poor at Stanford and intermediate at Mather. This is indeed one of the first field verifications of local adaptation by natural selection.

Correlation Among Characters

Given that *P. glandulosa* has 7 pairs of chromosomes, it is obvious that if ca. 100 genes are involved in the expression of the analyzed char-
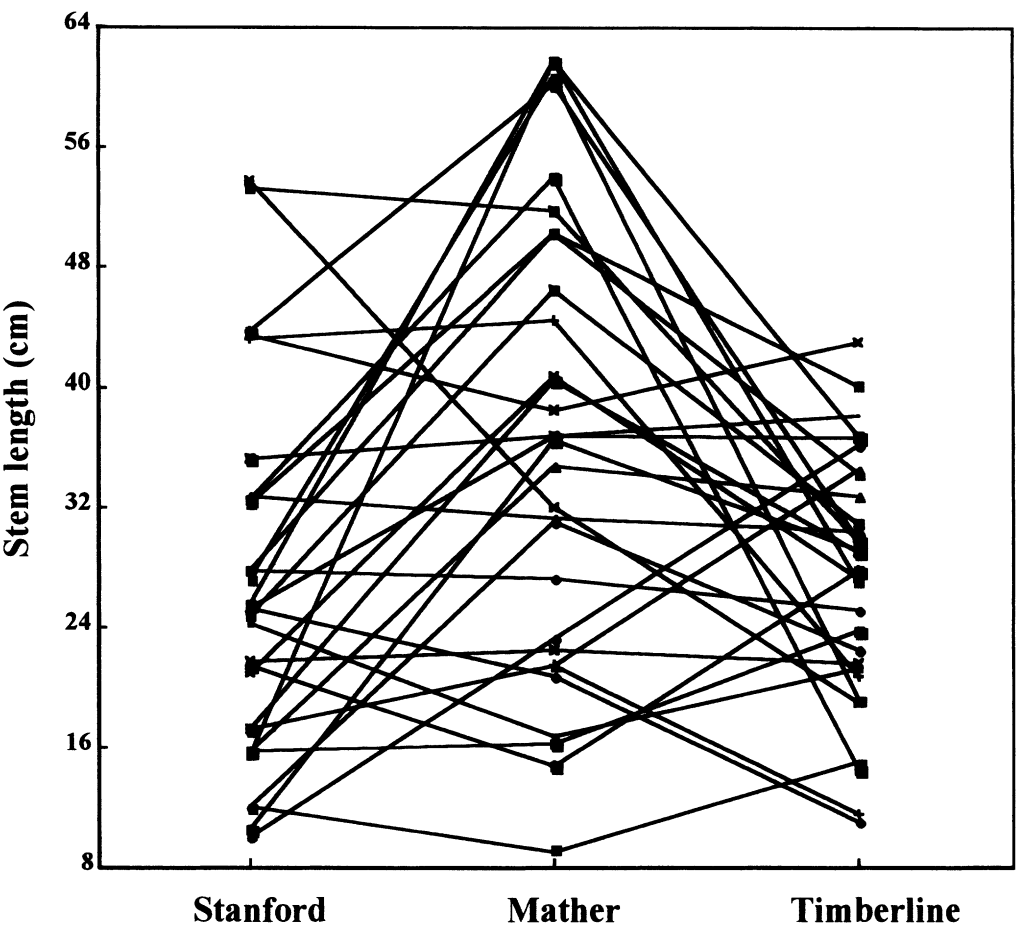
FIGURE 5.

Reaction norms of stem length of clones of different segregating F_2 plants derived from the cross between foothill (*reflexa*) and alpine (*nevadensis*) populations of *Potentilla glandulosa*, grown in different environments in Central California. (Data from Table 35 of Clausen and Hiesey 1958.)

acters, some of them must be linked. Clausen and Hiesey attempted to discern the genetic architecture of the characters by calculating broad-sense genetic correlations. They estimated correlations (r) for the traits of F_2 progenies. Because sample sizes were quite large, many correlations were significant (Table 2). They expected characters resulting from the same growth process to show strong correlation, probably due to pleiotropy. In contrast, correlation among functionally unrelated traits might be the result of linkage. Correlations were generally high among growth characters, intermediate among floral characters, and low

among physiological characters. The negative correlation ($r = -0.35$) between two fitness-related traits—early flowering and resistance to frost—suggested a trade-off in their adaptive value in reproduction and survival. In contrast, the correlation of notched petal, of no clear adaptive value and present only in Timberline plants, with frost resistance suggested linkage between genes of these traits.

Clausen and Hiesey hypothesized that if different character combinations were favored in specific environments, then changes in correlation (magnitude or direction) would be expected. They estimated correlations at each of
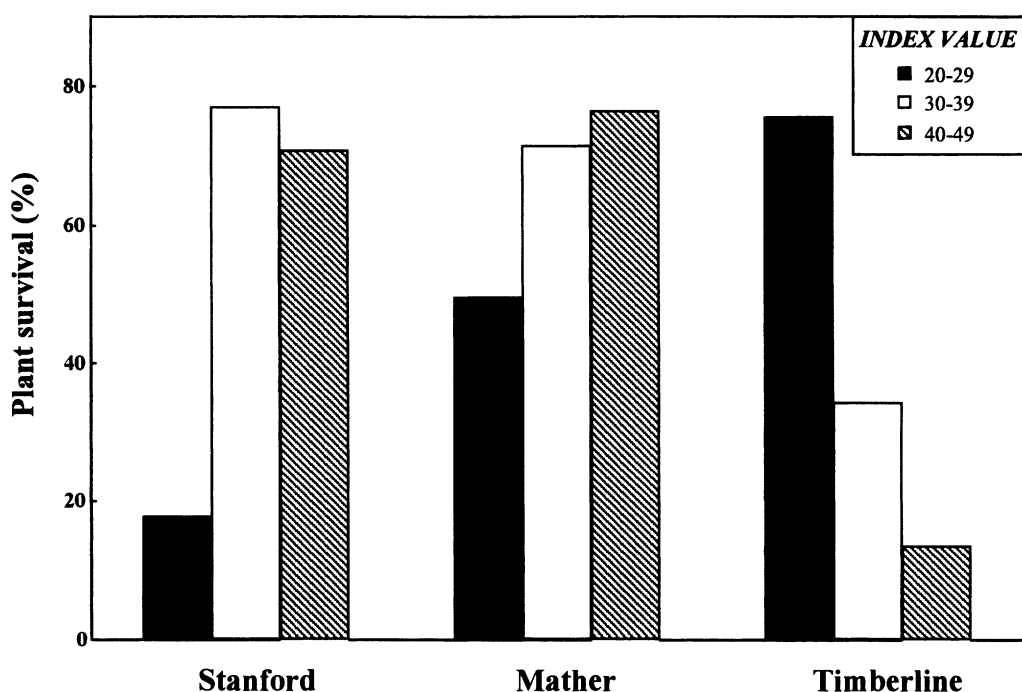
FIGURE 6.

A demonstration of natural selection in *Potentilla glandulosa*. Survival of F_2 genotypes with different index values (*IV*) in three different environments in Central California. Low *IV* indicate overall phenotypic similarity to alpine parent, high *IV* indicate overall phenotypic similarity to foothills parent. (Total sample size = 509; data from Table 47 of Clausen and Hiesey 1958.)

the three stations between vigor and flowering time and 14 other characters for F_2 plants. Five characters that were positively correlated with vigor at Stanford and Mather had negative correlations with vigor at Timberline. For instance, a strong negative correlation of frost susceptibility and vigor at Timberline indicated that frost resistant plants were generally short with small, narrow leaves; these characters were not correlated at either Mather and Stanford. Similarly, vigor was positively correlated with both stem and leaf length at Stanford and Mather, but weakly negatively correlated at Timberline. To Clausen and Hiesey, these results suggested that: (1) character correlation changes in magnitude and/or direction from population to population may result from differences in genetic architecture, and (2) selection preserved only certain types of combinations. Although this evidence regarding the role of selection on genetic variation is indirect (and

does not adjust for intertrait correlations), the approach was valuable in the absence of matching of phenotypes with specific polygenic genotypes.

Clausen and Hiesey's approach to the study of natural selection in the wild was remarkable. In the absence of simple polymorphisms they were able to demonstrate the genetic basis for population differentiation in *P. glandulosa* and its adaptive nature. They concluded that the abundant differentiation of populations and races of *P. glandulosa* had been driven by the results of "long-time selection," but acknowledged the potential for gene flow and introgression to provide raw material for new adaptive arrangements:

[Races] have attained an equilibrium with their environments. Natural selection will therefore tend to favor the original racial combination as long as the over-all genetic structure and the habitats remain the same

TABLE 2

Correlation among characters of F_2 plants of Potentilla glandulosa grown at Mather, derived from the F_1 of the cross Timberline Oak × Grove (subspecies nevadensis and reflexa, respectively)

Character	Stem	Leaf	Crown	Branch	Orient.	Notch	Color	Width	Length	Anth.	Frost
Stem height											
Leaf length	0.64										
Crown height	0.31	0.29									
Branching	0.42	0.31	0.32								
Orientation	0.07	0.06	0.19	0.04							
Notch	0.07	−0.02	0.19	0.13	0.13						
Color	0.01	0.26	0.19	0.07	0.21	0.15					
Width	−0.09	−0.01	−0.05	−0.10	0.29	0.11	0.17				
Length	−0.18	−0.00	0.09	−0.00	0.20	0.06	0.56	0.10			
Anthocyanin	0.24	0.07	0.16	0.32	0.02	−0.00	−0.05	−0.13	0.00		
Frost resist.	−0.01	−0.01	0.19	0.19	0.08	0.25	0.12	0.04	0.11	0.17	
Flowering time	−0.11	−0.22	0.02	0.04	−0.02	−0.01	0.05	0.12	0.06	0.07	−0.35

(Petal: Orientation, Notch, Color, Width, Length)

Correlations ≤ 0.087 are not significantly different from zero (at $P = 0.05$; data from Table 42 of Clausen and Hiesey 1958; note that there is no correction for multiple tests). In interpreting the sign of the correlation it is important to consider how the characters were scored. Scale of character scoring: stem (short to tall), leaf (short to long), crown (0–13 cm), branching (erect to divaricate), anthocyanin (green to red), frost resistance (resistant to susceptible), flowering (early to late); for petals: orientation (ascending to reflexed), notch (notched to entire), color (white to yellow), width (wide to narrow), length (long to short).

... Over long periods genes may gradually migrate across long distances ... and may finally appear in combinations where they have selective value (Clausen and Hiesey 1958:156).

Finally, despite their firm stance on the efficacy of selection at producing ecological races, they wondered about how such apparently intricate genetic systems might evolve, recognizing the tension between the apparent coherence of racial forms and the necessity for "flexible gene systems" (pp 266–267).

CKH AND THE "MODERN SYNTHESIS"

Mayr (1980) suggested that most biological disciplines (genetics, systematics, paleontology) adopted the *synthetic* view of evolution in the meeting held at Princeton in 1947. The main tenets of this synthesis were: (1) gradual evolution is brought about by small genetic changes and recombination; (2) natural selection is the main evolutionary process acting on random variation within populations; and (3) evolutionary phenomena associated with macroevolution and speciation are consistent with microevolutionary mechanisms (Mayr 1980). The works of CKH published prior to the Princeton conference, and those published subsequently, not only embodied the principles of the nascent synthesis, but often provided real data in support. So why were they not recognized?

THE ENVIRONMENT IN WHICH CKH WERE EXPRESSED

The early synthesis was "constructed" mainly by zoologically oriented naturalists who mostly left out botanical work (with some notable exceptions; e.g., Huxley 1942). It is difficult to identify all the "architects" of the synthesis, especially those with smaller contributions or research programs that embodied the basic tenets. Dobzhansky in 1937 (*Genetics and the Origin of Species*) was both in time and in scope the first true synthesizer: the evolutionary unit was the population, the main force was selection, evolution was gradual, and species were separated by physiological isolating mechanisms. Smocovitis (1997) has proposed that the synthesis arose from Dobzhansky's book and the subsequent three sets of Jesup Lectures at Columbia University that were published as books: Mayr (1942), Simpson (1944), and Stebbins (1950). Bennett (1964:57), however, mentions

a group of works of the 1930/1940s as advancing an "understanding of the relations between continuity and discontinuity, between populations and the forces of natural selection," which included not only the Jesup Lecture volumes, but also the books by C D Darlington (1939), de Beer (1940), Goldschmidt (1940), and Huxley (1942), as well as works by the Russian botanist Sinskaya and CKH (see also Futuyma 1998). "In fact and in tone—as well as in titles—these works were synthetic" (Bennett 1964:57).

Dobzhansky in *Genetics and the Origin of Species* (1937) appears to be the first to expose the evolutionary work of CKH. He mentions Clausen mainly in relation to cytogenetics: hybrids and variation of chromosome numbers in *Viola*, formation of chromosome rings in *Polemonium*, speciation through allopolyploidy in *Penstemon*. In his chapter "Selection," however, he refers to CKH in relation to the genetic basis of geographic differentiation and its bearing on adaptation (pp 169–170), specifying their work and that of Turesson on the genetic basis of local differentiation. For the third edition of his book in 1951, Dobzhansky described in detail the experiments, genetics, and reaction norm results for *Potentilla glandulosa* (in the chapter "Race formation," and in the section "Experiments on adaptedness of races in plants"). However, for other issues of plant evolution Dobzhansky relied now on Stebbins's book (see below).

In *Evolution: The Modern Synthesis*, Huxley (1942:437) assessed three works of CKH (1937, 1938, 1940), including *ESNOS I*. Indeed, Huxley's citation of *ESNOS I* is perhaps the first proper reference to their work in the Synthetic realm. Huxley referred to their conclusions in the chapter on "Adaptation and Selection," quoting the following paragraph from *ESNOS I*:

> The adaptive capacity (modificational plasticity) of coastal and alpine ecotypes is therefore insufficient to allow either to live and to compete in the habitat of the other. It is the difference in inheritance that enables them to succeed in their respective regions (Huxley 1942:437).

In addition, Huxley (p 441) cited particular results from *Potentilla*, *Achillea*, and *Aster* (cf. Figure 4): each has multiple ecotypes from a coastal range form to an alpine form, and each ecotype reacted differently when exposed to a range of environments. Huxley used these results to underscore a point about the complexity of interactions between genetic and modificational factors (i.e., differences in norms of reaction).

In *Systematics and the Origin of Species*, Mayr (1942), in the chapter "Nongeographic Speciation" (p 194), pulls a quote from the paper by Hiesey et al. (1942), "some taxonomists begin to wonder whether they are dealing with another species or merely with a variety or a subspecies," to deliver the message that it was not just zoologists that have problems with the concept of geographic and ecological races. Mayr, however, overlooked CKH's 1939 definition of biological species in plants, nor did he cite the thorough work of *ESNOS I* (1940) and its importance for adaptation. Furthermore, he does not cite CKH at all in his influential *Animal Species and Evolution* (1963), deferring to Stebbins's 1950 text for references to plant evolution (see below). This omission is especially surprising given that Mayr himself reviewed *ESNOS III* for the journal *Evolution*, and recognized it as one of the first attempts to generalize the adaptive nature of ecological differentiation in plants and animals:

> It is evident from these studies that there is no fundamental difference between plants and animals in the evolution of populations and races that have become adapted to local environments . . . The remarkable study of Clausen, Keck, and Hiesey on climatic races in *Achillea* could well serve as a model for similar investigations on other organisms (Mayr 1948:376).

THE BOTANICAL SYNTHESIS

G Ledyard Stebbins's *Variation and Evolution in Plants* (*VEP*; 1950) arose out of his Jesup Lectures at Columbia University in 1946. *VEP* was the first major review of botanical work to acknowledge the principles of the synthesis, and the scope of topics alone make this a remarkable achievement. Mayr (1980:132) and others, however, have christened *VEP* as the first truly "synthetic" work in botany. If this were true, the synthetic view arrived rather late for botanists. In fact, work previous to this was truly synthetic (Bennett 1964; Stebbins 1980), but *VEP* has been so influential that

most other work has received scant attention. In fact Stebbins acknowledged in *VEP* that synthetic work in botany was *ongoing*:

> The present book is intended as a progress report on this synthetic approach to evolution as it applies to the plant kingdom . . . It does not intend to offer any new hypotheses, except on certain limited phases of plant evolution (Stebbins 1950:ix).

Stebbins's own work at this time was focused on cytogenetics, polyploidy, and apomixis, and later on species complexes and hybridization; his contribution at the 1947 Princeton meeting was on rates of evolution in plants (Stebbins 1949). Indeed, the populational thinking that is a tenet of the synthesis (and a hallmark of the work of CKH) is scarce in Stebbins's own work, and in *VEP* only one of 14 chapters (Chapter IV) is devoted to selection and adaptation at the population level. In fact, at that time, the best evidence for selection and adaptation, and isolating mechanisms in plants, was available from the works of CKH. Stebbins relied heavily on important ideas from both CKH's *American Naturalist* paper (1947) and *ESNOS III* (1948) in his section on microevolution.

Stebbins cited 20 works of the Clausen group in *VEP*, including the first three volumes of *ESNOS*. The 40+ entries in the index that refer to the Carnegie group is second in importance only to Stebbins's own 63 entries. Stebbins also included diagrams from the work of CKH in *VEP*. Stebbins reviewed Clausen's 1951 book *Stages in the Evolution of Plant Species*, and although at odds with Clausen for interpretation of some data, he comments, "it must be ranked as one of the most important contributions to our understanding of plant evolution which has appeared in recent years" (Stebbins 1952:132). Stebbins's (1980) later recollection of botanical contributions to the synthesis is seemingly at odds with these earlier views. He mentions the importance of CKH's early results, but makes repeated reference to their dearth of publications, which he attributed to Clausen's perfectionism. Clausen's book receives only this mention: "The only publication of their work on species is a short book published by Clausen in 1951" (Stebbins 1980:143). Thus, although Stebbins lauded some of their findings, he did not credit them with the vision

of a synthesis that seems apparent to us (see also Schlichting and Pigliucci 1998).

VISIBILITY OF CKH

Were their results disseminated widely enough? It is possible that the Carnegie Institution volumes were not readily accessible to students of evolution. However, CKH published three papers that contained summaries of *ESNOS* results in the *American Naturalist* in the 1940s: those in 1941 and 1942 dealt with *ESNOS I* and *ESNOS III*, and the 1947 paper included preliminary results of *ESNOS IV*, as well as new results on *Hemizonia* and *Layia*. Hiesey published results of further experiments on *Achillea* in *Evolution* in 1953. In 1951, Clausen published the book, *Stages in the Evolution of Plant Species*. In it he uses the patterns of differentiation represented by various species, subspecies, and races to "reconstruct" evolutionary processes. There are significant discussions of the work on tarweeds, as well as reviews of the results of *ESNOS I–III* and previews of *ESNOS IV*. Throughout, it is clear that, in Clausen's view, microevolutionary mechanisms are fully adequate to explain most instances of plant speciation.

Did CKH interact with colleagues? Each of the above *American Naturalist* papers resulted from symposium presentations by the authors at national meetings. In fact, the 1947 paper was delivered by Clausen at the inaugural meeting of the Society for the Study of Evolution in December 1946, and he frequently attended the International Congress of Genetics. CKH were also the founders, in 1936, of the Biosystematists, a San Francisco Bay area discussion group with interests in evolution; other early members included Stebbins, Ernest Babcock, Herbert Mason, and Richard Goldschmidt (Smocovitis 1994, 1997; Lidicker 2000).

CONCLUDING REMARKS

It is clear that the research program carried out by CKH from 1932 embraced a "synthetic" (or, more properly, a comprehensive) view of the evolution of plant species. Most botanical studies of the time were centered on species formation via polyploidy; adaptation, however, was little studied (reviewed by Huxley 1942; Clausen et al. 1948:117–121; see also Stebbins 1950; Briggs and Walters 1984). The dis-

tinctive research program of CKH to explicitly investigate adaptation led to the results that produced their view of evolution as a gradual process. CKH's goal of studying natural selection in the field, by itself, is of considerable importance. Some critics of the synthesis have argued that proponents of the synthesis have failed to investigate whether adaptation and selection actually occurred in nature (Gould and Lewontin 1979; Antonovics 1987). However, to paraphrase Antonovics (1987:330), CKH were already eager to "dissect the unicorn" even as the synthesis was unfolding.

CKH were clearly of the adaptationist school as seen by their focus on confirming the action of natural selection—the process that they hypothesized was responsible for the adaptive physiological differences among ecotypes and climatic races. Their demonstration of natural selection in *Potentilla glandulosa* was especially consequential because, although the Synthesis proposed natural selection as the major evolutionary process, few studies had been done in animals or plants (see Morley 1959; Provine 1986:343; Antonovics 1987), nor had good experimental methods been developed (see Morley 1959; Futuyma 1998). However, even recent reviews (e.g., Endler 1986) have not included the work on *P. glandulosa* in *ESNOS IV*, although it may represent the first explicit study of natural selection on plants in the field.

Another revolutionary aspect of the work of CKH was their analysis of the genetic structure of populations. They detected large quantities of continuous genetic variation for fitness-related traits, estimated the numbers of genes governing their inheritance, and observed how various genotypes reacted to different environments. Furthermore, they proposed that natural selection favors certain combination of characters (and genes). The studies of CKH fall into what Wright (1981) called "organismic" rather than "genic" selection; that is, selection acting on the genetic architecture. Wright, however, did not cite these accomplishments in his reviews on population variation in quantitative characters (1968) or his reviews on population structure and differentiation (1978).

That CKH pushed forward their investigations on *Potentilla glandulosa*, even after demonstrating that most characters had polygenic

control, is crucial. Distinctive polymorphisms were highly sought after for evolutionary studies because their simple genetic control systems were amenable to population genetic analysis. Such systems (e.g., *Biston*, *Cepaea*, *Linanthus*, and *Panaxia*) became the battleground between adherents of Fisherian and Wrightian views on the relative importance of selection and genetic drift for population differentiation (Provine 1986, 1992), and dominated evolutionary investigation for decades until quantitative genetic analysis successfully crossed over into evolutionary studies.

CKH's inductive approach, searching for patterns in the masses of data collected on an astonishing variety of plant species, certainly had none of the spectacle produced by the battles between the Fisher and Wright camps. Like Dobzhansky, their focus was on understanding the genetics of natural populations; unlike Dobzhansky, for whom data were only interesting in relation to testing theory (Provine 1986:347), CKH believed that the complexity of natural systems precluded tests of the contemporary evolutionary theory. In a short but revealing passage, Clausen and Hiesey present an understated critique of population genetics. Taking note of the Fisher-Wright controversy, they argued that, given that "the genetic systems these formulas assume are far too simple to represent correctly the operation of actually existing systems," in natural populations, it was "premature to discuss the relative merits of formulas that are designed to by-pass a detailed genetic analysis" (Clausen and Hiesey 1958:159).

Most evolutionary biologists today recognize that in order to understand population differentiation, speciation, adaptation, or coevolution, they cannot ignore the role of the environment in gene expression. The idea of reaction norms, although traceable to the German researcher Woltereck in 1909, introduced to the synthesis by Dobzhansky (1937) and later championed by Schmalhausen (1949), was not applied to natural populations until the work of CKH (Lewontin 1983). CKH, in perfecting the transplant methodology of Turesson, devised a means of investigating the environment-dependent nature of phenotypic expression of their clonal genotypes. Their data from the multiple transplant gardens are among

the earliest to provide evidence of genotype by environment interaction. In this context, Clausen and Hiesey envisioned a much more sweeping scope for ecological genetics than that proposed by Ford: (1) the analysis of genes which control the inheritance of individual characters of populations; (2) understanding the expression of genes in different environmental conditions; and (3) mapping the pathways or mechanisms through which genes act to produce their observed phenotypes in diverse environments. That this perspective was proposed in 1958 makes its modern flavor all the more remarkable!

Most of the topics that CKH explored from the 1930s through the 1950s are still areas of active research in both plant and animal systems. Mechanisms of speciation (Whitkus et al. 2000; Knowles 2001) are as avidly discussed as ever. Studies of polyploidy (Otto and Whitton 2000; Soltis and Soltis 2000) and hybridization and transgressive segregation (Ellstrand and Schierenbeck 2000; Steen et al. 2000; Schwarzbach et al. 2001) are enjoying a revival. Analysis

of the genetic control of phenotypes is burgeoning as new methods are developed (Oldham et al. 2000; Poncet et al. 2000; Klingenberg et al. 2001). Careful investigations of local adaptation (Donohue et al. 2000; Poore and Steinberg 2001) and reaction norms (Relyea 2001; Sultan 2001) are plentiful. And, finally, the study of selection in natural populations (Mousseau et al. 2000) has reemerged to share the stage with experimental research (Bennett and Lenski 1999).

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