Invited Papers

from the 14th Annual Meeting
Winnipeg, July 1977

Edited by Jennifer M. Shay

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CANADIAN BOTANICAL ASSOCIATION

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INTRODUCTION

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This supplement to the Bulletin includes three major papers delivered at the 1977 meetings of the Canadian Botanical Association in Winnipeg. We were privileged to have Dr. Peter Raven, the Director of the Missouri Botanical Garden as our plenary speaker. His lecture was entitled "*Hybridization and the Nature of Species in Higher Plants*". The other two papers by Dr. R.T. Coupland and Dr. J.C. Gilson were contributions to the symposium, "*Prairie destiny use, conservation, reclamation*".

In his paper on hybridization in higher plants, Dr. Raven focuses upon the adaptation and evolution of plant populations and compares the hybridization potential of annuals and perennials. The latter constitute almost ninety percent of the world's vascular flora and have relatively few barriers to hybridization. The emphasis on vegetative reproduction in perennials and the selective value of sexual reproduction in bringing together a range of genetic material is discussed. Interfertility, among perennial species such as *Epilobium* may well have been a dominant characteristic in their evolution, allowing them to effectively exploit new habitats as these became available. In contrast, annuals, exemplified by *Clarkia*, show little tendency to produce fertile hybrids, a feature linked with both morphological and physiological characteristics. Dr. Raven emphasizes that a 'common ecological role' is an important factor in holding species together. He closes by suggesting that the evaluation of coadapted gene complexes in local populations at the biochemical-physiological level may be a fruitful avenue for future research.

It seemed natural that the CBA/ABC Conference held in Winnipeg should choose a prairie theme for its major symposium. Within the broad framework of prairie destiny, four topics were selected - prairie ecology; economics; water resources and eutrophication; and genetic resources. Unfortunately, the day before the meeting Dr. C. Person, the speaker for the last topic, was unable to attend; his paper and the one by Dr. J. Vallentyne on water resources are not included in this supplement.

It is difficult, even for those of us who live in the west, to visualize the nature of the prairies before the coming of the Europeans. Scattered accounts by early explorers and travellers provide a glimpse of the once unbroken sea of grass that stretched nearly a thousand miles from the edge of eastern forests to the foothills of the Rockies. That the grasslands were rich in game is testified to not only by these early descriptions but also by the fact that it was rarely difficult for the mobile native populations to make a good living off this natural bounty. Even by modern estimates, the original bison population must have numbered in the millions, not to mention elk, deer, wolf, grizzly bear and a host of other animal species. It is only recently that substantive studies of natural prairie productivity have been carried out under the aegis of the International Biological Program and other agencies, allowing us to appreciate the productivity of natural grassland. As our insights into natural grassland dynamics expand, it is inevitable that comparisons will be made between these and our carefully managed croplands.

Dr. Coupland was the co-ordinator of Canada's I.B.P. Matador Grassland project. In his paper on "*Prairie Ecology*" he reviews immigration, the development of agriculture with the introduction of widespread cultivation and grazing, the so-called "improvement" of the land, and the extinction of buffalo herds. Increases in population and industrial expansion followed rapidly and the western Canadian grasslands became one of the most modified biomes in the world. After discussing some of the problems associated with agricultural use of semi-arid grassland, Dr. Coupland focuses upon productivity and the inputs necessary for high yields, both in cultivated and range land. He emphasizes the need to preserve segments of grassland as reference sites for comparison of managed and natural productivity. In this connection, it is to be hoped that the proposed Grassland National Park near Val Marie in southern Saskatchewan, will soon be established.

parently accelerated by summerfallowing (to which practice a third of our croplands are assigned each year). Who knows what additional more subtle changes are taking place in cropland soils? It seems necessary to revert to less exploitive procedures to protect the productive capacity that remains. This suggests the need for greater inputs by chemicals to control pests, another area which causes concern for the future health of cropland ecosystems and of organisms dependent on them.

In order that we may be in a position in the future to assess the degree of deterioration in our managed ecosystems, it is essential that we maintain some reference areas in a natural state. If experience shows that management regimes are failing to sustain productivity of croplands and rangelends, such reference areas will be invaluable as a basis for understanding what types of modifications will be advisable in management inputs. Great care must be taken to assure that selected areas are protected on a perpetual basis. Through the Canadian contribution to the International Biological Program candidate areas have been selected and much effort has been expended in arranging for protection. This must continue until success is achieved through the passage and implementation of adequate legislation. Hopefully, management procedures in the proposed Grassland National Park in southern Saskatchewan will be such as to protect some natural grassland in perpetuity against the ravishing effects of agriculture, urbanization, strip mining, road building, and the extraction of petroleum products.

References

Coupland, R.T. 1974. Conservation of grasslands. In Conservation in Canada: a Conspectus. (eds. J.S. Maini and A. Carlisle). Canada Department of the Environment, Canadian Forestry Service, Pub. No. 1340. Ottawa.

Johnston, A. 1970. A history of the rangelands of western Canada. J. Range. Management, 23: 3-8.

Johnston, A. and Smoliak, S. 1977. The potential of Canada's forage crops. Agrologist, 6(2): 10-13.

Mondor, C. 1976. The Canadian plains: the vanishing act. Nature Canada, 5(2): 32-39.

Morton, A.S. and Martin, C. 1938. History of Prairie Settlement and Dominion Lands Policy. Vol. II of Canadian Frontiers of Settlement (eds. W.A. Mackintosh and W.L.G. Joerg). The MacMillan Co. of Canada Ltd., Toronto.

Murchie, R.W. 1936. Agricultural Progress on the Prairie Frontier. Vol. V of Canadian Frontiers of Settlement (eds. W.A. Mackintosh and W.L.G. Joerg). The MacMillan Co. of Canada Ltd., Toronto.

Shields, J.A., Rostad H.P.W. and Clayton, J.S. 1970. Inventory of Saskatchewan Soils and their Capability for Agricultural Use. A.R.D.A. Pub. M13, Sask. Inst. of Pedology, Univ. of Sask., Saskatoon.

HYBRIDIZATION AND THE NATURE OF SPECIES IN HIGHER PLANTS

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Starting almost three decades ago, many scientists began to feel a degree of disillusionment with the concepts of biosystematics (Raven, 1974; 1977b), a field then about twenty years old. Since that time, several lines of investigation have suggested that this feeling was based mainly on the difficulties associated with inadequate models of species, speciation, and hybridization, which earlier had given the false promise of universality in their application to the studies of plant populations. Even though G.L. Stebbins warned in his landmark book, Variation and Evolution in Plants (Stebbins, 1950), of the difficulties of carrying out evolutionary studies effectively in a taxonimic context, many continued the attempt to apply such essentially theoretical concepts as that of the so-called "biological species" to real-world situations and thereby to "reform" a taxonomic system increasingly seen as artificial.

Further conceptual and practical advances have suggested new lines of investigation and have again made the study of plant populations in nature both respectable and productive. Among these are the following:

1. A growing realization of the extreme local nature of plant populations, and the consequent limited evolutionary significance of "gene flow" (e.g., Levin and Kerster, 1974, 1975; Raven, 1977a).
2. A better understanding of the nature of linkage and homeostasis, and of the conditions under which single genes or gene complexes can be substituted in populations. This might be characterized as a gradual shift from single-locus to multilocus thinking in population genetics (e.g., Clegg, Allard, and Kahler, 1972; Raven, 1978).
3. Increased knowledge of molecular genetics and developments that have, in principle, allowed us to study the nature of local adaptation in plant populations (Solbrig et al., 1978; Raven, 1978).
4. An increased appreciation of the role of hybridization in the adaptation and evolution of plant populations, a topic that will constitute the main subject of this paper.

Hybridization in Plants

Owing to the ease of cultivating and experimentally manipulating plants, their hybrids have interested horticulturists and botanists for a very long time. In plants, it has been easier than in animals to check the results of hypotheses concerning the evolutionary implications of hybridization. More than 250 years of experimental hybridization of plants and, of course, extensive observations in the field, have formed the basis for the results and conclusions reviewed here (see also Raven, 1977b).

The first experimental hybrid in plants to be reported was apparently that made by Thomas Fairchild, a commercial flower-grower of London, between Dianthus barbatus L. and D. caryophyllus L., reported in 1717 (Zirkle, 1935). Linnaeus discussed plant hybrids and made at least one himself, between Tragopogon porrifolius L. and T. pratensis L., reporting the results in 1760. The next year, 1761, the German J.G. Kölreuter, working in the garden of the Academy of Sciences in St. Petersburg, reported more than 500 different plant hybrids he had made in his classic Vorläufige Nachricht. In 1849, Carl Friedrich von Gärtner published an encyclopedic work, Versuche und Beobachtungen über die Bastarderzugung im Pflanzenreich. In this he not only recorded nearly 10,000 separate experiments involving some 750 different species of plants that yielded some 250 different hybrids, but also, in strikingly "biosystematic" terms, devised an "index of affinity" between species as the proportion of the number of seeds produced following an interspecific pollination to the number produced following a conspecific one.

Results from artificial or natural hybridization in plants have naturally affected the concepts of species held by botanists. Linnaeus and his contemporaries in the 18th century, of course, regarded species as the special works of the Creator. Later, the English botanist William Herbert, writing in 1837, made it clear that the general opinion of the day was that if two entities when hybridized produced fertile offspring they ought to be considered the same species. Herbert rejected this point of view himself, pointing out that "if two species are to be united in a scientific arrangement on account of a fertile issue, the botanist must give up his specific distinctions generally and entrench himself within the general." Thus, with a fairly extensive practical knowledge about the limits to hybridization of plants, botanists were fairly sophisticated about the nature of the units they called species well before 1900. They have generally viewed efforts to introduce a so-called "biological" species concept in plants with misgiving because of the nonoperational character of such definitions.

There is, of course, an obvious and direct relationship between the concept of species and that of hybrids; the definition of one is entirely dependent upon the definition of the other. In this connection, a comment by J.D. Hooker (1855) is particularly illuminating: "In the course of our extended wanderings, it has been our habit to acquaint ourselves with the plants as we gathered them, and so to observe their differential characters in the field, that we were never at a loss for the means of understanding one another when alluding to any particular species, yet we never met with a plant that suggested to us even a suspicion of hybridisation..." In contrast, a current inventory of the flora of the British Isles (Stace, 1975a, 1975b) records some 850 documented interspecific hybrids in a flora of about 2250 species, and one that was very well known to Hooker at the time he was writing the flora from which the quotation just mentioned was drawn. Above all, the demonstrated relationship between prior hypothesis and subsequent conclusion should serve to alert us to the dangers of attempting to interpret patterns in nature too rigidly from a certain viewpoint, a criticism that might be applied to the application of the formal taxonomic system itself (see, for example, Raven, Berlin, and Breedlove, 1971; Raven, 1977b).

The high water mark of efforts to define plant species experimentally came in 1940, when J. Clausen, D.D. Keck, and W. Hiesey (1939, 1940) attempted to establish as universal categories of classification ecotype, ecospecies, and coecospecies to replace the traditional ones. By 1951, however, Clausen had evidently concluded that these experimentally defined categories were, in fact, yardsticks by which to measure natural variation, and not operational taxonomic units. In his influential book of 1950, Stebbins pointed out clearly the need to separate species definition, however constructed, from the study of evolutionary processes, and most botanists today espouse a pragmatic view of the nature of classification, and of the reasons for constructing a taxonomic system. The prevalent view has been articulated well by Davis and Heywood (1963).

The Role of Hybridization in Perennial Plants

In most woody plants and perennials, which constitute some 87 percent of the flora of the world, barriers to hybridization between the units morphologically, ecologically, and physiologically recognized as species are relatively few and mainly external. Although sections and relatively distantly related species are usually intersterile -- for example in Picea (Wright, 1955) and Populus (cf. Zsuffa, 1973; Willing and Pryor, 1976) -- more closely related species can usually be hybridized to give fertile progeny. The external barriers to hybridization that characterize woody and perennial species of higher plants can be recognized mainly when the species involved are sympatric. Many of them are K-strategists which devote a relatively low proportion of their basic resources to sexual reproduction. Among them, the ability to hybridize may actually have a selective value, as suggested by Epling (1947). This possibility, and the patterns characteristic of such groups, will be explored with examples drawn mainly from four genera: Epilobium, Scaevola, Bidens, and Ceanothus.

Epilobium (Onagraceae) is a genus almost entirely composed of perennial herbs, and one that is nearly worldwide in distribution. In New Zealand, there are some 37 native species of sect. Epilobium (Raven and Raven, 1976), whereas in North America, where the genus almost certainly originated, there are approximately 24 (P.C. Hoch and Raven, unpubl.). An extensive program of hybridization amongst the New Zealand species has shown that all are interfertile, and that although they are extremely diverse morphologically and ecologically, they hybridize readily where they come together in nature. The genus appears to have reached New Zealand no more than a few million years ago, and to have radiated rapidly in the newly formed, expanding, and diverse alpine and subalpine habitats of these islands (Raven, 1973; Raven and Raven, 1976). The ready dispersibility of the comose seeds of Epilobium, combined with the pervasive autogamy of the plants once established, has carried them to all relatively open habitats and led to the perpetuation of specific adaptive sets of characteristics in them (Raven and Raven, 1976, p. 46-47).

The recombination of genetic material from populations of Epilobium in New Zealand produces, both in the experimental garden and in the field, populations that are sometimes better suited for survival in particular habitats than either parent. In other words, the whole of the genetic diversity of sect. Epilobium in New Zealand is available for what might be called interspecific recombination. Such wide recombination makes available for selection a much wider array of genotypes than could be produced within a particular population or series of populations at a given adaptive mode. This appears to have played an extremely important role in allowing Epilobium to have exploited the diverse subalpine and alpine habitats in New Zealand rapidly (in a geological sense) and efficiently (in an ecological sense). Thus, the recombination of genetic material from somewhat differentiated populations, followed by the maintenance of well adapted genetic strains by a combination of autogamy and habitat preference, seems to have been the dominant theme in the evolution of Epilobium in New Zealand.

The genus Scaevola (Goodeniaceae) on the Hawaiian Islands illustrates the role of hybridization as a part of the adaptive system in a group of woody plants (Gillett, 1966). Of the seven species found in Hawaii, Scaevola gaudichaudiana H. & A. is widespread on the lowlands of Oahu, Molokai, Lanai, and Kauai, and is one of the few native species that can hold its own with the aggressive weedy flora that flourishes there. It is a glabrous shrub or small tree with white flowers, fruits 3-4 mm in diameter, peduncles 40-60 mm long, and 0-15 hydathodes along each side of the midvein. In the sopping wet rainforests at higher elevations on Oahu occurs Scaevola mollis H. & A., which differs from S. gaudichaudiana in being sericeous, with violet flowers, fruits 8-9 mm in diameter, peduncles 3-15 mm long, and 25-40 hydathodes along each side of the midvein.

These two very different species come together on the Koolau Range of Oahu and hybridize to produce a variable series of intermediate populations. The variation in the Scaevola gaudichaudiana complex throughout the four islands where it occurs parallels that observed where S. gaudichaudiana and S. mollis come together on Oahu. Within this group, 19 formal taxonomic descriptions have been accorded to such populations, incuding six species, seven varieties, and six forms. One of these, for example, is the series of populations that has been called S. procera Hillebrand, which occurs at higher elevations on Kauai (Carlquist, 1970, p. 151-155). All of these, however, are best understood as intermediates between two distinct species, some recently produced, and others of greater antiquity. Since intermediates between S. gaudichaudiana and S. mollis occur on three islands where S. mollis is absent, one must either hypothesize that it once occurred on these islands or subsequently became extinct, or that its fleshy, bird-dispersed fruits provided a means by which hybrids formed on Oahu could reach the other islands. If they were suited by their physiological characteristics to the conditions found there, they might then persist and form the populations seen at the present time. Of course, climatic change since the last Pleistocene pluvial maximum has been extensive, and must be taken into account in interpreting the patterns observed at the present day.

Another group of Hawaiian plants that illustrates a similar pattern of variation on an even more extensive scale is the genus Bidens (Asteraceae; Gillett and Lim, 1970; Gillett, 1972a, 1972b, 1973, 1975; Mensch and Gillett, 1972). A variable assemblage of plants of this genus occurs throughout the Hawaiian Islands from sea level to about 1800 m elevation. All but one of these species are members of sect. Campylotheca, divided by E.E. Sherff, the monographer, into some 43 species, 42 in Hawaii and one in the Marquesas. All of these species are high polyploids, $2n = 72$, and all of the Hawaiian ones that have been tested are interfertile. Given the great differences between populations in this group and their interfertility, it is not surprising that hybrids were often accorded specific status. Gillett (1975) positively identified 10 of the named species as hybrids, reconfirming many of the results from his study of field populations by experimental hybridization. Given the very wide morphological variation exhibited by artificial and natural hybrids in this complex, it is not surprising that taxonomists have divided the complex into nearly four dozen species. Based on his results in the field and laboratory, Gillett (1975) proposed that the entire species of populations in Hawaii be treated as a single species with seven intergrading subspecies.

Although we tend to think of the extent and meaning of hybridization on islands as somehow different from that which occurs in continental areas, there is little evidence that this is the case. Woody plant groups that have been studied in detail afford numerous examples of interfertile species, poorly developed barriers in hybridization, and ecological/seasonal differentiation being most important in separating species. One need only mention Cupressus, Eucalyptus, Magnolia, Picea, Populus, and Quercus to make the point. Although barriers to hybridization certainly exist within all of these groups, and are of intense interest for understanding their evolution and in seeking improved strains for the purposes of forestry, what we are emphasizing here is the potential of the hybridization itself in affording new recombinants for the exploitation of novel habitats or in adjusting to climatic change. The process is illustrated especially well by Ceanothus sect. Cerastes of California and neighboring areas.

Hybrids between the two sections of Ceanothus are obtained only with great difficulty, and there are very few natural populations that are suspected to have had originated following intersectional hybridization (Nobs, 1963). Within sect. Cerastes, however, there appear to be no barriers to hybridization, and intermediates occur whenever morphologically distinct populations come together in nature. Although species such as Ceanothus cuneatus (Hook.) Nutt. and C. gloriosus J.T. Howell or those between C. jepsonii Greene and C. ramulosus (Greene) McMinn differ widely in flower color, leaf size and margin, habit, and ecology, they are interfertile and produce an impressive array of recombinants in the F_2 generation. The evolutionary implications have been stated well by Nobs, and can be understood in the context of the complex geology of the North Coast Ranges of California.

In this region, Nobs (1963) studied in detail the relationships between 11 species of this section, and found that they occurred on a wide variety of substrates. Two were restricted to serpentine, five to Pliocene Sonoma volcanics of varied composition, and one to Franciscan Cretaceous marine sandstones. Within this complex environmental mosaic, the ability of species of sect. Cerastes to produce hybrid recombinants better suited to particular combinations of ecological factors than either parent as the climate changed since the middle Pliocene has doubtless given the group a great adaptive advantage. Such varied ecological situations became more frequent in the North Coast Ranges from the Pliocene onward as tectonism increased. The evolutionary opportunities afforded led to a multiplication of species in this restricted area in a group of plants that has been widespread in drier scrubland and woodland communities in North America since at least Middle Miocene time (17 m.y. ago), when precursors of both the entire-leaved C. cuneatus and the tooth-leaved C. crassifolius were in existence (Axelrod, 1939). Many other genera of woody and perennial plants, such as Arctostaphylos, seem to display a similar pattern in this region (Raven and Axelrod, 1978, p. 78-81), but again, it should be stressed that patterns of this sort are nearly universal among woody and perennial plants, although they appear to be accentuated under certain ecological circumstances.

Introgressive hybridization (Anderson, 1949, 1953) is a term used to describe the movement of genetic material from one species into another across a genetic barrier without weakening the barrier in the process. Subsequent to its original formulation, the concept has been used to describe many situations involving hybridization between differentiated populations -- so many so that it probably is no longer a useful term (Heiser, 1973; Raven, 1977a). Even the best known examples often seem not to conform to Anderson's original definition when they are studied in detail; e.g., Asclepias tuberosa L. (Wyatt, 1977), Helianthus (Olivieri and Jain, 1977), Juniperus (Flake, von Rudloff, and Turner, 1969; Adams, 1977). In its original formulation, introgressive hybridization appears to have depended upon a fixed idea of the integrity of species and the implicit notion that if they were modified by hybridization, they must still somehow have remained constant. In fact, it now appears that there exists in nature a continuous array of situations resulting from hybridization, which appears best to be described as an integral part of the genetic system of higher plants, expecially in woody and perennial groups, but also under certain circumstances in annuals (e.g., Raven, 1960, 1962; Bloom, 1976). If the hybrids are particularly favored in specific ecological situations, asexual reproduction, polyploidy, or simply autogamy may favor the perpetuation of specific genotypes through a narrowing of the spectrum of genetic recombination characteristic of the population. No general conclusions about the most appropriate way to treat these populations taxonomically appear to be possible.

Hybridization in Annual Plants

Among the annuals, which comprise some 13 percent of the flora of the world, the modal pattern of differentiation is quite distinct (Raven, 1977b). The well studied genus *Clarkia* appears to be a good example of the patterns of differentiation characteristic of annual plants (Onagraceae; Lewis, 1953a, 1953b; Lewis and Lewis, 1955). There are 43 species of *Clarkia*, one of central Chile and adjacent Argentina, and all but one of the remainder in California. A few species range beyond the borders of California and one, *C. pulchella* Pursh, is restricted to the northwestern United States and extreme southern British Columbia. Of the 43 species, 33 are diploid, with aneuploid changes in chromosome number having evolved in relation to adaptation to aridity (Lewis, 1953b).

Up to several species of *Clarkia* often occur sympatrically, yet hybrids are very rare in the wild. Some species can be crossed to produce hybrids under experimental conditions, but most of these hybrids are highly sterile and all have strongly reduced fertility. Much of the sterility has been related to chromosomal repatterning between species. The difficulty of obtaining interspecific hybrids certainly contributes to the maintenance of outcrossing species growing together, for the flowers of these highly colonial plants are visited primarily by bees that are oligolectic on *Clarkia* but do not discriminate, for the most part, on a species-by-species basis, despite the conspicuous floral differences the plant species display (MacSwain, Raven, and Thorp, 1973).

Interchange heterozygosity is frequent in naturally occurring individuals of many species of *Clarkia*, and hybrids between populations or even individuals within populations may also exhibit sterility, sometimes even complete sterility (Lewis, 1953a, p. 6). Although the barriers that separate species are generally based upon more extensive chromosomal reorganization, there is a continuum among hybrids between differentiated populations from complete fertility to almost complete sterility. If differentiated populations do come together, they may be maintained as distinct and preserve unique combinations of morphological and physiological characteristics.

In some outcrossing species of *Clarkia*, such as *C. dudleyana* (Abrams) Macbr. (Snow, 1960) and *C. arcuata* (Kell.) Nels. & Macbr. (Snow and Imam, 1964), no one chromosomal arrangement is widespread, and populations are differentiated from one another chromosomally; in others, including *C. amoena* (Lehm.) Nels. & Macbr. (Snow, 1963) and *C. unguiculata* Lindl. (Mooring, 1958), the species is characterized by one widespread chromosomal arrangement, with other arrangements being more local. Natural populations of all four species display high frequences of translocations, whereas in other outcrossing species of *Clarkia*, such as *C. rubicunda* (Lindl.) Lewis & Lewis (Bartholomew, Eaton, and Raven, 1973), *C. biloba* (Dur.) Nels. & Macbr. (Lewis and Roberts, 1956), and the diploid species of sect. *Myxocarpa* (Small, 1971b), strict chromosomal homozygosity is prevalent. The reasons for these differences are obscure, but the way in which they are related to the structure of genetic diversity presumably is the key to understanding their significance (cf. Bloom, 1977).

The evolution of reproductive barriers in *Clarkia* can be illustrated well by the eight diploid and one tetraploid taxa of sect. *Myxocarpa* (Small, 1971a, 1971b). Very few populations of most of the diploid taxa have been investigated experimentally, and all eight diploids are allopatric. The physiological differences in terms of adaptation to drought are impressive (Small, 1972a), and not fully correlated either with morphological differentiation or with reproductive isolation (Small, 1972b). In the widespread tetraploid *Clarkia rhomboidea* Dougl., a series of 26 populations from throughout the range of the species exhibited a wide array of interfertilities as measured by pollen stainability in F_1 individuals (Mosquin, 1964). Their fertilities were partly correlated with chromosomal rearrangements between the strains.

A different pattern is that of the entirely diploid *Clarkia unguiculata* complex, in which at least four derivative species are sharply separated from the parental *C. unguiculata* and from one another by sterility barriers (Vasek, 1964a, 1968a). Many crosses within *C. unguiculata* (Mooring, 1958), and one of its derivatives, *C. exilis* Lewis & Vasek (Vasek, 1958, 1960), were nearly as fertile as their parents; but, as in sect. *Myxocarpa*, the taxonomy has been oriented strongly to the presence of sterility barriers. The four derived species related to the largely outcrossing (Vasek, 1965) *Clarkia unguiculata* are much more autogamous than it (e.g., Vasek, 1964b, 1968b; Vasek and Harding, 1976) and probably derived from it by saltational speciation very recently. They are adapted to environments more xeric than those inhabited by their ancestral species, *C. unguiculata* (Vasek, 1964a), and all bloom earlier than that species in nature, an obvious adaptation to the earlier onset of summer heat and drought in their habitats (Vasek and Sauer, 1971).

Similar examples of the derivation of marginal populations by saltational speciation have been documented for *Clarkia lingulata* Lewis & Lewis (Lewis and Roberts, 1956; Gottlieb, 1974) and for marginal populations of *C. xantiana* A. Gray (Moore and Lewis, 1965). *Clarkia franciscana* Lewis & Raven, on the other hand, does not appear to be derived directly from *C. rubicunda* as initially assumed (Lewis and Raven, 1958; Gottlieb, 1973). Aneuploid changes in chromosome number often accompany adaptation to more xeric marginal situations in *Clarkia* (Lewis, 1953b).

In other genera of annual plants, few of which have been studied as extensively as Clarkia, the patterns appear similar (e.g., Raven and Axelrod, 1978, for California). Strong internal barriers to hybridization often characterize the morphological, physiological, and ecological units recognized as species, but also often separate individual populations, many of which are not obviously distinctive in other respects (Raven, 1977a). Barriers to hybridization appear to arise principally as a byproduct of the process of differentiation (Stebbins, 1950; Grant, 1958, 1971; Levin, 1971), and more rapidly in annuals, which are relatively r-selected, than in perennials. The continued distinctiveness of outcrossing species of annuals, which must reproduce by seed each year, appears to depend more directly upon barriers to hybridization than does the maintenance of comparable distinctiveness among perennials, in which very few seeds may actually be involved in the production of mature individuals.

Whether selection for stronger barriers to hybridization takes place in plants when differentiated populations are sympatric ("character displacement") remains to be seen. Such selection for reproductive isolation has been claimed by Grant (1966) for annual species of Gilia; he termed such selection the "Wallace effect." On the other hand, such differences can arise by chance, as argued by Valentine (1953) for Primula, and it is difficult to be sure of the reasons for stronger or weaker reproductive isolation between different pairs of species. Patterns of this sort have been reported for Clarkia (Abdel-Hameed, 1971), Fuchsia (Breedlove, 1966), and Phlox (Levin and Kerster, 1967), but they do not appear to be frequent in the higher plants. The utter complexity of one of the first-reported cases of character displacement, in the avian genus Sitta, has been documented beautifully by P.R. Grant (1975); and the difficulties of interpretation involved in it would certainly suggest caution in ascribing similar explanation to observed patterns in other groups.

The Evolution of Species in Higher Plants

Of fundamental importance to the understanding of speciation in higher plants is a growing sense of the indeterminacy of the process. There is very little evidence in plants for the classical model of speciation by the separation of formerly continuous populations, as espoused by Dobzhansky and Mayr, among the leaders of contemporary evolutionary thought, although it may be the rule in other groups, such as birds (cf. Diamond, 1977). Endler (1977) has recently presented a remarkable analysis of the problem of differentiation in relation to geographical isolation, and his productive conclusions are at variance with the rigid application of the allopatric model of speciation. The severe limitations on gene flow as it is actually observed in nature, and the intensive nature of adaptation to the local environment exhibited by populations of organisms, have made it evident over the past 20 years that the species should not be regarded as a fundamental unit of evolution except in terms of relationships (Ehrlich and Raven, 1969; Raven, 1977a). For plants at least, the uncritical acceptance of typological statements such as that recently published by M.J.D. White (1978, p. 3) -- "It cannot be emphasized too strongly that every species is at the same time a reproductive community, a gene pool, and a genetic system" is highly misleading as a guide for the interpretation of populations in nature (cf. Harper, 1977, p. 751). Even if such a concept has been used to formulate the existing taxonomy of Drosophila, of birds, and of a few other groups, and can therefore be used in a circular fashion to describe the resulting taxonomy, it certainly has a very limited general applicability. What is needed is more experimental work, not repeated assertions about the structure of populations and population systems in living organisms.

When Jens Clausen was writing his very useful book, Stages in the Evolution of Plant Species, published in 1951, he recognized this interdeterminacy in annuals such as Holocarpha and Layia, but thought of it as exceptional. Writing about Clarkia shortly thereafter, Lewis (1953a) pointed out that in the variable populations of this genus, morphologically and physiologically distinct strains were constantly arising. Because of the prevalence of translocation heterozygosity in Clarkia, many were also reproductively isolated; a few were successful in some ecological role, and became the species or differentiated races we see in nature. Later, Lewis (1962, 1966, 1973) added the concepts of catastrophic selection and saltational speciation to account for the founder principle, White's (1978) "stasipatric" speciation, or Carson's ideas of the evolution of Hawaiian Drosophila from a single individual founder (Carson, 1971, 1973, 1975).

Although Harlan Lewis, writing 25 years ago, thought this mode of speciation might be unusual -- perhaps characteristic only of Clarkia and a few similar groups -- it now appears that the translocations and reproductive isolation were simply the mechanism that made a common evolutionary process stand out more sharply. There appears to be little evidence yet for plants at least to accept as a generality the conclusion of White (1978), that chromosomal rearrangement normally precedes the differentiation of those populations that ultimately are recognized as species. On the other hand, some sort of imperfectly understood reorganization of the populations does appear to be necessary. Additional observations both within and between species will be essential to test the validity of White's idea.

In both annuals and longlived plants, it is likely that selection for better adapted populations in a mosaic environment continually provides a supply of evolutionary novelties. A few of these, especially if they are suited to novel or marginal ecological conditons, become successful. Reproductive isolation is neither necessary nor an inevitable end point for plant species, and interspecific hybridization itself may be a highly adaptive and nearly universal feature of population systems in plants, especially in those with longer generations.

In many ways, the normal mechanism of speciation in plants as just described appears to be highly compatible with the evolutionary pattern described in the field of paleobiology as the theory of punctuated equilibria (Gould and Elridge, 1977; Avise, 1977). Individual local populations acquire a set of distinctive and adaptive characteristics, through a very wide variety of evolutionary mechanisms, and then some of them spread and by doing so become the forerunners of the next order of differentiation (Clausen, 1951). Whole geographically isolated races presumably become distinctive largely by the same process: the spread of a novel genotype, perhaps largely by replacement, over a new area, and the elimination of less well adapted individuals. Differentiated races of "semispecies" of plants "are not always, and perhaps not usually, species *in statu nascendi*" (Stebbins, in Dobzhansky *et al.*, 1977, p. 223). The appearance and spread of differentiated entities in plants seems to depend on "genetic revolutions" -- whatever the full implications of that term may be -- in local populations. Geographical differentiation, hybridization, polyploidy, asexual reproduction and autogamy contribute in various ways to the speed with which such genetic revolutions can be carried out in a particular set of circumstances.

Viewed in this light, no particular observed pattern in nature can logically be regarded as the precursor of any other. For example, ecotypes (cf. Quinn, 1978), races, subspecies, and "semispecies" (as pointed out by Baum, 1972) cannot be regarded as stages in the evolution of species. Rather they are seen as taxonomic evaluations of particular patterns of variation in nature which are themselves the product of the interplay between the genetic diversity of the populations involved and the environment. Each is thought to have originated in a single population at a particular place, and then to have spread to its present area; apparent exceptions to this generality have probably usually been explained in terms of convergent or parallel evolution. Sterile plants produced by hybridization between populations may persist indefinitely if their habitat persists. There is no *a priori* reason why they, or any other pattern of variation observed in natural populations, should be selected for or against in a particular set of ecological circumstances. Annuals may change more rapidly than perennials, and are often subject to drastic changes in their environments (cf. Schaeffer and Gadgil, 1975), but the differentiation of distinctive entities, occupying new adaptive peaks, appears to be similar in all plants.

In this view of evolution, species seem to be held together chiefly by their possession of a common ecological role, as postulated by Darwin over a centuty ago (Raven, 1978). Novelties arise in local populations continuously and in very large numbers, and a few -- those which are adapted to a particular, previously unexploited environment that has, by reason of climatic change or migration of a propagule, become available -- give rise to new differentiated series of populations after their origin at a particular place. The rapidity of speciation in such situations as oceanic islands or in regions where recent drastic climatic shifts have taken place (e.g., mediterranean climates, newly uplifted mountains) is related to the appearance of new or fundamentally altered environments in these areas, but the underlying evolutionary phenomena appear identical to those elsewhere. For the further elucidation of this "common ecological role," and more understanding of the process of differentiation of those distinctive units that we recognize as taxonomic entities, the evaluation of coadapted gene complexes in local populations at the biochemical-physiological level appears to offer the most promise.

Literature Cited

Abdel-Hameed, F. 1971. Cytogenetic studies in *Clarkia*, section *Primigenia*. V. Interspecific hybridization between *C. amoena huntiana* and *C. lassenensis*. Evolution 25: 347-355.

Adams, R.P. 1977. Chemosystematics-analyses of populational differentiation and variability of ancestral and recent populations of *Juniperus ashei*. Ann. Missouri Bot. Gard. 64: 184-209.

Anderson, E. 1949. Introgressive Hybridization. New York.

_____. 1953. Introgressive hybridization. Biol. Rev. Cambridge Philos. Soc. 28: 280-307.

Avise, J.C. 1977. Is evolution gradual or rectangular? Evidence from living fishes. Proc. Natl. Acad. Sci. U.S.A. 74: 5083-5087.

Axelrod, D.I. 1939. A miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash. Publ. Biol. 516: 1-129.

Bartholomew, B., L.C. Eaton, and P.H. Raven. 1973. *Clarkia rubicunda*: a model of plant evolution in semiarid regions. Evolution 27: 505-517.

Baum, B.R. 1972. *Avena septentrionalis*, and the semispecies concept. Can. J. Bot. 50: 2063-2066.

Bloom, W.L. 1976. Multivariate analysis of the introgressive replacement of *Clarkia nitens* by *Clarkia speciosa polyantha*. Evolution 30: 412-424.

_____. 1977. Translocation heterozygosity, genetic heterozygosity, and inbreeding in *Clarkia speciosa*. Evolution 31: 256-264.

Breedlove, D. 1969. The systematics of *Fuchsia* section *Encliandra* (Onagraceae). Univ. Calif. Publ. Bot. 53: 1-69.

Bush, G.L., S.M. Case, A.C. Wilson, and J.L. Patton. 1977. Rapid speciation and chromosomal evolution in mammals. Proc. Natl. Acad. Sci. U.S.A. 74: 3942-3946.

Carlquist, S. 1970. Hawaii, A Natural History. Garden City, New York.

Carson, H.L. 1971. Speciation and the founder principle. Univ. Missouri Agric. Exp. Sta. Stadler Genet. Symp. 3: 51-70.

_____. 1973. Reorganization of the gene pool during speciation. Pop. Genet. Monogr. 3: 274-280. Honolulu.

_____. 1975. The genetics of speciation at the diploid level. Amer. Naturalist. 109: 83-92.

Clausen, J. 1951. Stages in the Evolution of Plant Species. New York.

_____, D.D. Keck and W. Hiesey. 1939. The concept of species based on experiment. Amer. J. Bot. 26: 103-106.

_____, _____, & _____. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Publ. Carnegie Inst. Wash. 520: i-vii, 1-452.

Clegg, M.T., R.W. Allard, and A.L. Kahler. 1972. Is the gene the unit of selection? Evidence from two experimental plant populations. Proc. Natl. Acad. Sci. U.S.A. 69: 2474-2478.

Davis, P.H. and V.H. Heywood. 1963. Principles of Angiosperm Taxonomy. Edinburgh.

Diamond, J.M. 1977. Continental and insular speciation in Pacific land birds. Syst. Zool. 26: 263-268.

Dobzhansky, T., F.J. Ayala, G.L. Stebbins, and J.W. Valentine. 1977. Evolution. San Francisco.

Endler, J.A. 1977. Geographic Variation, Speciation, and Clines. Princeton, N.J.

Flake, R.H., E. von Rudloff, and B.L. Turner. 1969. Quantitative study of clinal variation in *Juniperus virginiana* using terpenoid data. Proc. Natl. Acad. Sci. U.S.A. 62: 487-494.

Gärtner, C. 1849. Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreich. Stuttgart.

Gillett, G.W. 1966. Hybridization and its taxonomic implication in the *Scaevola gaudichaudiana* complex of the Hawaiian Islands. Evolution 20: 506-516.

_____. 1972a. Genetic affinities between Hawiian and Marquesan *Bidens* (Asteraceae). Taxon 21: 479-483.

_____. 1972b. Additional experimental crosses in Hawaiian *Bidens* (Asteraceae). Pacific Sci. 26: 415-417.

_____. 1973. Genetic relationships between *Bidens forbesii* and six species in the Hawaiian and the Marquesas Islands. Brittonia 25: 10-14.

_____. 1975. the diversity and history of Polynesian *Bidens*, section *Campylotheca*. Howard L. Lyon Arboretum Lecture No. 6: 1-32.

_____ and E.K.S. Lim. 1970. An experimental study of the genus *Bidens* in the Hawaiian Islands. Univ. Calif. Publ. Bot. 56: 1-63.

Gottlieb, L.D. 1973. Enzyme differentiation and phylogeny in *Clarkia franciscana*, *C. rubicunda* and *C. amoena*. Evolution 27: 204-214.

_____. 1974. Genetic confirmation of the origin of *Clarkia lingulata*. Evolution 28: 244-250.

Gould, S.J. and N. Eldridge. 1977. Punctuated equilibria: The tempo and mode of evolution reconsidered. Paleobiology 3: 115-151.

Grant, V. 1958. The regulation of recombination in flowering plants. Cold Spring Harbor Symp. Quant. Biol. 23: 337-363.

_____. 1966. The selective origin of incompatibility barriers in the plant genus *Gilia*. Amer. Nat. 100: 99-118.

_____. 1971. Plant Speciation. New York.

Grant, P.R. 1975. The classical case of character displacement. Evol. Biol. 8: 237-337.

Harper, J.L. 1977. Population Biology of Plants. London.

Heiser, C.B. Jr. 1973. Introgression reexamined. Bot. Rev. (Lancaster) 39: 347-366.

Herbert, W. 1837. Amaryllidaceae; preceded by an attempt to arrange the Monocotyledonous orders, and followed by a treatise on cross-bred vegetables, and supplement. London.

Hooker, J.D. 1855. Flora Indica. Vol. 1. London.

Kölreuter, J.G. 1761. Vorläufige Nachricht von einigen des Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen. Leipzig.

Levin, D.A. 1971. The origin of reproductive isolating mechanisms in flowering plants. Taxon 20: 91-113.

_____ and H.W. Kerster. 1967. Natural selection for reproductive isolation in *Phlox*. Evolution 21: 679-687.

_____ and _____. 1974. Gene flow in seed plants. Evol. Biol. 7: 139-220.

Lewis, H. 1953a. The mechanism of evolution in the genus *Clarkia*. Evolution 7: 1-20.

_____. 1953b. Chromosome phylogeny and habitat preference in *Clarkia*. Evolution 7: 102-109.

_____. 1962. Catastrophic selecton as a factor in speciation. Evolution 16: 257-271.

_____. 1966. Speciation in flowering plants. Science 152: 167-172.

_____. 1973. The origin of diploid neospecies in *Clarkia*. Amer. Nat. 107: 161-170.

_____ and M.E. Lewis. 1955. The genus *Clarkia*. Univ. Calif. Publ. Bot. 20: 241-392.

_____ and M.R. Roberts. 1956. The origin of *Clarkia lingulata*. Evolution 10: 126-138.

_____ and P.H. Raven. 1958. Rapid evolution in *Clarkia*. Evolution 12: 319-336.

MacSwain, J.W., P.H. Raven, and R.W. Thorp. 1973. Camparative behavior of bees and Onagraceae. IV. *Clarkia* bees of the western United States. Univ. Calif. Publ. Entom. 70: 1-80.

Mayr, E. 1942. Systematics and the Origin of Species. New York.

Mensch, J.A. and G.W. Gillett. 1972. The experimental verification of natural hybridization between two taxa of Hawaiian *Bidens* (Asteraceae). Brittonia 24: 57-70.

Moore, D.M. and H. Lewis. 1965. The evolution of self-pollination in *Clarkia xantiana*. Evolution 19: 104-114.

Mooring, J. 1958. A cytogenetic study of *Clarkia unguiculata*. I. Translocations. Amer. J. Bot. 45: 233-242.

Mosquin, T. 1964. Chromosomal repatterning in *Clarkia rhomboidea* as evidence for post-Pleistocene changes in distribution. Evolution 18: 12-25.

Nobs, M.A. 1963. Experimental studies on species relationships in *Ceanothus*. Publ. Carnegie Inst. Wash. 623: 1-94.

Olivieri, A.M. and S.K. Jain. 1977. Variation in the *Helianthus exilis-bolanderi* complex: A reexamination. Madrono 24: 177-189.

Quinn, J.A. 1978. Plant ecotypes: Ecological or evolutionary units? Bull. Torrey Bot. Club 105; 58-64.

Raven, P.H. 1960. Interspecific hybridization as an evolutionary stimulus in *Oenothera*. Proc. Linn. Soc. London 173: 92-98.

_____. 1962. The systematics of *Oenothera* subgenus *Chylisma*. Univ. Calif. Publ. Bot. 34: 1-122,

_____. 1973. The evolution of subalpine and alpine plant groups in New Zealand. New Zealand J. Bot. 11: 177-200.

_____. 1974. Plant systematics 1947-1972. Ann. Missouri Bot. Gard. 61: 166-178.

_____. 1977a. Systematics and plant population biology. Syst. Bot. 1: 284-316.

_____. 1977b. The systematics and evolution of higher plants. *In* Goulden, C.E. (ed.), Changing Scenes in Natural Sciences, 1776-1976, p. 59-83. Academy of Natural Sciences, Philadelphia, Spec. Pub. 12. Lancaster, Penn.

_____. 1978. Future directions in plant population biology. *In* Solbrig *et al.* (ed.), The Population Biology of Plants. Columbia

Univ. Press, New York (in press).

______ and D.I. Axelrod. 1978. Origin and relationships of the California flora. Univ. Calif. Publ. Bot. 72: 1-134.

______, P. Berlin and D.E. Breedlove. 1971. The origins of taxonomy. Science 174: 1210-1213.

______ and T.E. Raven. 1976. The genus *Epilobium* (Onagraceae) in Australasia: A systematic and evolutionary study. New Zealand Dept. Sci. Industr. Res. Bull. 216: 1-321.

Schaffer, W.M. and M.D. Gadgil. 1975. Selection for optimal life histories in plants. *In* M.L. Cody and J.M. Diamond (eds.), Ecology and Evolution of Communities, p. 142-147. Cambridge, Mass.

Small, E. 1971a. The systematics of *Clarkia*, section *Myxocarpa*. Can. J. Bot. 49: 1211-1217.

______. 1971b. The evolution of reproductive isolation in *Clarkia*, section *Myxocarpa*. Evolution 25: 330-346.

______. 1972a. Adaptation in *Clarkia*, section *Myxocarpa*. Ecology 53: 808-818.

______. 1972b. Tempo of adaptive change during the rapid evolution of chromosomal isolates. Taxon 21: 559-565.

Snow, R. 1963. Cytogenetic studies in *Clarkia*, section *Primigenia*. I. A cytogenetic survey of *Clarkia amoena*. Amer. J. Bot. 50: 337-348.

______ and A. Imam. 1964. Cytogenetic studies in *Clarkia*, section *Primigenia*. II. A cytological survey of *Clarkia arcuata* and *Clarkia lassenensis*. Amer. J. Bot. 51: 160-165.

Solbrig, O.T., S.K. Jain, G.B. Johnson, and P.H. Raven (eds.). 1978. The Population Biology of Plants. Columbia Univ. Press, New York (in press).

Stace, C.A. (ed.). 1975a. Hybridization and the Flora of the British Isles. London.

______. 1975b. Wild hybrids in the British flora. *In* S.M. Walters (ed.), "European Floristic and Taxonomic Studies." p. 111-125. Faringdon.

Stebbins. G.L. 1950. Variation and Evolution in Plants. New York.

Valentine, D.H. 1953. Evolutionary aspects of species differences in *Primula*. Symp. Soc. Exper. Biol. 7: 146-158.

Vasek, F.C. 1958. The relationship of *Clarkia exilis* to *Clarkia unguiculata*. Amer. J. Bot. 45: 150-162.

______. 1960. a cytogenetic study of *Clarkia exilis*. Evolution 14: 88-97.

______. 1964a. The evolution of *Clarkia unguiculata* derivatives adapted to relatively xeric environments. Evolution 18: 26-42.

______. 1964b. Outcrossing in natural populations. I. The Breckinridge Mountain population of *Clarkia exilis*. Evolution 18: 213-218.

______. 1965. Outcrossing in natural populations. II. *Clarkia unguiculata*. Evolution 19: 152-156.

______. 1968a. The relationships of two ecologically marginal, sympatric *Clarkia* populations. Amer. Nat. 102: 25-40.

______. 1968b. Outcrossing in natural populations: A comparison of outcrossing estimation methods. *In* Drake, E.T. (ed.). Evolution and Environment, p. 369-386. New Haven, Conn.

______ and J. Harding. 1976. Outcrossing in natural populations. V. Analysis of outcrossing, inbreeding, and selection in *Clarkia exilis* and *C. tembloriensis*. Evolution 30: 403-411.

______ and R.H. Sauer. 1971. Seasonal progression of flowering in *Clarkia*. Ecology 52: 1038-1045.

White, M.J.D. 1978. Modes of Speciation. San Francisco.

Willing, R.R. and L.D. Pryor. 1976. Interspecific hybridization in poplars. Theor. Appl. Genet. 47: 141-151.

Wright, J.W. 1955. Species crossability in spruce in relation to distribution and taxonomy. For. Sci. 1: 319-349.

Wyatt, R. 1977. Population dynamics and reproductive biology of butterflyweed, *Asclepias tuberosa* L. Ph.D. Dissertation, Duke Univ., Durham, N.C.

Zirkle, C. 1935. The Beginnings of Plant Hybridization. Philadelphia.

Zsuffa, L. 1973. A summary review of interspecific breeding in the genus *Populus* L. Proc. 14th Meeting Can. Tree Improv. Assoc. 2: 107-123.

PRAIRIE ECOLOGY

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Before agricultural settlement of the prairie provinces, grassland occupied about 100 million acres. It is difficult to be precise because the forest margin has advanced in the black soil zone since the landscape has been protected from fires that were wide-ranging and recurrent prior to settlement. I have suggested (1974) that the area of open grassland was between 90 and 100 million acres, while Johnston and Smoliak (1977) have estimated the area at 115 million acres by assuming that it was coincident with the total area of the brown, dark brown and black soil zones. The greatest modification to the prairie landscape has been caused by agricultural activities. Accordingly, it seems appropriate to review the extent to which changes have resulted from various uses of land, as a basis for predicting the nature of these prairie landscapes in the future.

Immigration and Agricultural Development

At the beginning of the 19th Century cultivation was limited to gardens at fur trading posts, where a few milk cows were also maintained after being imported in freighter canoes as calves. The first agricultural settlement was at Fort Garry (now Winnipeg) beginning in 1812. Many difficulties beset the early settlers and it was not until about 10 years later that the herds of livestock began to grow at a steady pace after restocking by animals that were trailed from the south. There were serious limitations to the production of crops because of the difficulties of export. Accordingly, before the arrival of the railway, agricultural development did not expand much beyond that required for maintenance of the colony and the fur trading posts.

Agricultural settlement began in earnest in southern Manitoba in the 1870s, in anticipation of the arrival of the railroads (Morton and Martin, 1938). The first railroad arrived from the south in 1878 and was soon followed by one from the east which was built as far west as Brandon in 1881. At that time Brandon marked the western extremity of agricultural settlement. The railway crossed the rest of the prairies as far as Calgary by 1883 and branch lines developed soon thereafter, reaching Saskatoon and Edmonton in 1890 and 1891, respectively. The land adjacent to the railroads was the first occupied for arable agriculture. By 1900 corridors of occupied farmland embracing the railroads formed a network across the prairies, which by 1910 (during the decade of greatest settlement activity) had filled the spaces between the railroads (Murchie, 1936).

Meanwhile, in the ranching country in the southwestern prairies, cattle ranching on the open range began in the 1870s (Johnston, 1970). As a prelude to ranching on an extensive basis, several changes took place. Notable were the extinction of the buffalo herds (which assisted in efforts to confine the natives to reservations) and the coming of law and order with the entrance into the region of the Mounted Police. By the 1890s the rapid expansion of ranching was brought to a halt by competition for land among farmers.

The most severe modification of the natural landscape has resulted through the cultivation of land for crop production. The greatest rate of expansion in the area of "improved" land (cropland, summerfallow, seeded pasture and farmyards) took place in the first three decades of this century when the average annual increase was 1.8 million acres and resulted in an increase from 5.5 million acres in 1901 to 59.8 million acres in 1931 (Fig. 1). Subsequently, the average rate of increase in area of improved land decreased to 700,000 acres per year in the next four decades and to 190,000 acres annually during the first half of the present decade, so that the total area "improved" was 88.6 million acres in 1976. About three-quarters of this cultivated land in the prairie provinces is located in the grassland zone.

The other great agricultural impact on the landscape has been through the grazing of domesticated animals. In Figure 2 I have have converted populations of livestock into animal units. These values indicate that the grazing pressure increased very rapidly from 1901-1921, when it reached the equivalent of 4.4 million animal units. There was a decline in grazing pressure during the next three decades to 3.1 million animal units. This was followed by another increase which resulted in a grazing pressure that exceeded the peak of 1921 during the 1960s and reached 5.8 million by 1976. The major cause of the decline from 1921 to 1951 was a decrease in the population of horses, which were no longer depended upon as the chief source of motive power in the farming operation. Since 1951 the major cause of the increased grazing load has been expansion of the beef cattle industry, which has seen a more rapid rate of increase than at any previous time in our history.

The major increases in the human population took place between 1901 and 1931, when it climbed by 1.9 million (65,000 per annum), and since 1951 when it increased by another 1.2 million (an average of 50,000 per year) to a total of 3.8 million in 1976. The earlier increase was associated largely with agricultural settlement, while the latter is related to industrial expansion. A measure of the extensive influence of agriculture in the prairie provinces is indicated by the fact that by 1951 there were 28 acres of improved land per capita. Although this value has declined in the prairie provinces as a whole since 1951, it continued to increase in Saskatchewan to reach 50 acres per person by 1971. In comparison, the mean cultivated acreage per person in the world is less than 1 acre. Similarly, at the beginning of the present decade our population of cattle, sheep and goats (which was equivalent to 1.3 animal units per capita) was about four times the world average.

Impact of Settlement on Land Resources

Mondor (1976) has suggested that probably nowhere in the world has man so rapidly altered a biome as in the western Canadian grasslands. If there is another region, probably it is northern Kazakstan where all of the conversion of grassland to cropland ("the New Lands") took place in a period of about five years during the 1950s. The western Canadian experience was devastating. A deliberate government policy of bison slaughter began in earnest in 1865 and was complete about 1877. The elk population was also virtually exterminated. By 1905 government programs were underway to prevent complete elimination of bison and pronghorn. Two national parks were designated for the protection of bison. These were Buffalo National Park, which was established in 1908 and closed in 1940, and Elk Island National Park, which was opened in 1913. In 1922 three national parks were established for the protection of pronghorn, but only one of these was fenced and the arrangements were terminated as early as 1930 in one and 1947 in the last to survive.

Less interest has been given to protecting grassland vegetation than in protecting forest vegetation. Presumably this is because the canopy of grassland is replaced annually, while that of forest requires many years. However, grassland can be severely damaged by burning and heavy grazing so that its character changes very markedly. The time taken for recovery to a fully natural situation may not be much less than that required to develop a new forest canopy. It may take as long as five years for full recovery even from one fire.

Productivity of Land

The two alternatives for agricultural use of land in a semiarid to dry subhumid grassland region are as rangeland and as cropland. Evaluations of some of the earlier explorers resulted in parts of the Canadian prairies appearing in early maps as the northern extension of the "American Desert". We seem to have been very venturesome in extending arable agriculture so rapidly in a region where the fluctuations in weather are such as to cause extreme periodic aridity.

Cultivation of cropland on the prairies has permitted abundant harvests of grains, but at the expense of declining fertility of the soil. In cropland in southern Saskatchewan annual biological production (amount of energy fixed) is probably less than half that in natural grassland. Perhaps as little as a third as much energy is available (after harvest) to run the system, and the rate of decay is apparently much faster. As a result, the organic content of cropland is decreasing. The apparent greater production of cropland is the result of a higher harvestable yield of shoots at one time. The seemingly low, but actually higher, production of natural grassland results from growth over a much longer period (April to November), growth every year (no summerfallow), and the transference of much more of the production underground. The fact that leaves only survive for part of the growing season in native grassland causes few to be present as green material at any one time. Annual seeded crops develop their stems all at the same time and are harvested before leaves fall to the ground.

Recently much emphasis has been placed on increasing plant growth on rangelands by ploughing and seeding to such exotic perennial grasses as crested wheat grass and Russian wild rye. These are planted in open stands to reduce competition and increase their height. Forage yields of these stands are considerably greater for several years after seeding than those of natural grassland (however, comparisons of biological productivity have not been made). These increases in yield have usually been explained on the basis of the higher growth potential of the exotic species. However, similar increases in yield have been obtained by seeding to native species or by disturbing the native sod by tillage operations that permit survival of native grasses and make seeding unnecessary. It is evident, therefore, that the early surge of vigorous shoot growth following seeding is due to the tillage operation which increases the amount of available nutrients by speeding up the decay process.

The greater harvestable yield in cropland is achieved at the expense of management inputs (fossil fuel, pesticides, fertilizer). The greater the management inputs the greater the energy use per unit of harvestable product and the more unstable the system becomes. Also, as the intensity of management continues, the more dependent the system becomes on continuing and increasing inputs in order to maintain an acceptable level of crop yield. This is the basis of modern agriculture -- the greater the input, the greater the output, but the lower the efficiency of energy used in relation to unit of output.

Native grassland can be utilized for the production of domesticated livestock with a minimum of management inputs, but with a low harvestable return. Sustainability of rangeland production can be achieved by control of the number of livestock that graze per unit area of land. If grazing is too intensive the vegetation deteriorates and if this continues the soil is exposed and erodes. Consequently, moderate intensities of grazing are indicated for sustainable use of land as rangeland. In natural grassland in southern Saskatchewan, where (at the rate of grazing recommended by the Canada Department of Agriculture) the annual energy intake by cattle in the form of forage is calculated to be 147 kcal/m^2, that retained as animal tissue (gain in weight) is 9 kcal. In contrast, an estimated average of 349 kcal/m^2 is being diverted annually to human use from wheat fields on the same type of soil. Thus, it seems important that we consider if there are not ways in which the return from rangeland could be increased and still maintain the health of the ecosystem. On the other hand, about 2.5 times as much energy is being left after harvest to run the rangeland ecosystem than the cropland. We do now know what proportion of net plant production is required to run an ecosystem in the grassland region of western Canada, but there is abundant evidence (from declining levels of organic matter content in the soil) that the returns to the ecosystem are not sufficient in cropland.

We must not assume that our croplands will continue to produce indefinitely at a reasonable rate because of experience elsewhere. Indeed, the croplands of the Great Plains have been under cultivation longer than those of any semi-arid grassland zone. There is no experience elsewhere to use as a basis for estimating the degree of sustainability of our cropland resources. Non-irrigated lands that have been cultivated for hundreds of years are located in a more favourable climate than ours and they have been improved by intensive management inputs rather than exploited.

Future Land Use

Until about 1940 the area of occupied farm land in the prairie provinces increased faster than the area of "improved land" (at an average annual rate of 1.2 million acres in the first four decades of this century). After that, the situation reversed because the pressure to cultivate more land was greater than the supply of new land to be occupied. So, during the next four decades the area of "unimproved" (i.e., uncultivated or unbroken) land on farms declined at an average annual rate of 97,000 acres). This trend accelerated in the first half of the present decade to an average rate of 174,000 acres. While this loss of the natural landscape may not seem to be significant (it would take 260 years to plow it all at this rate), there are several reasons for concern. The proportion of land cultivated is already much greater than in other regions in which intensive agriculture is practiced. Even in the Netherlands only 59 percent of the land is under cultivation, compared to 65 percent of our farmland (which includes Crown land under lease). If we included community pastures, parks and Indian reserves within the settled area in the calculation, the proportion would be less, but still greater than that of the Netherlands. However, the intensity of the tillage is greater here with 92 percent of the cultivated land cultivated annually, compared to only 37 percent in the Netherlands. We leave one-third of our annually-cultivated land exposed to erosion as summerfallow, which further increases the risk of deterioration. Nevertheless, the rate at which new land is being broken is accelerating. This new land is that which has survived tillage because of its marginal or submarginal capability for crop production. As such, there are strong arguments for protecting it against exploitive uses which cannot be sustained.

The uncultivated farm land is used by ranchers and farmers as grazing land for domesticated livestock. The increasing grazing load and the decreasing area of grazing land is stimulating an interest in increasing the carrying capacity of the remaining rangeland. The major "improvement" practice being applied is conversion of natural grassland to seeded pasture by tillage and introduction of such exotic grasses as crested wheat grass and Russian wild rye. This program is being encouraged, and sometimes subsidized, by government agencies. The ARDA surveys have suggested that this is an appropriate procedure for land in Soil Capability Class No. 5 of the Canada Land Inventory. This will have a very significant impact in reducing the area of grassland that still remains untilled. In the Brown Soil Zone of Saskatchewan, for example, 78 percent of the uncultivated land is Class 5 (values for the Dark Brown and Black Soil Zones are 64 and 62 percent, respectively (Shields et al., 1970). No one can predict what proportion of this land will be ploughed and seeded. Certainly topographic features, salinity, stoniness and sandiness would seem to be dissuading factors to even those who ignore aridity; but even if only 50 percent of Class 5 land now remaining untilled is eventually converted to seeded pasture, only 17 percent of the landscape in the grassland zone of Saskatchewan (Brown, Dark Brown and Black Soil Zones) will have escaped the plough. These remaining natural and semi-natural areas will be saline flats, sandhills and rocky moraines.

I have two concerns with respect to this trend of conversion of native rangeland to seeded grassland. The first relates to the destruction of the natural ecosystem. This is a stable system supporting many plant species that survived all adversities of environment in presettlement time. With good managemnt, it is sustainable as a grazing resource and should only be destroyed if it is replaced by another sustainable system. The second concern relates to the fact that this conversion is being undertaken on the basis of observed increases in forage yield in the short-term, but without consideration of the long-term implications. Of particular note is the interpretation that the early increases in yield after ploughing and seeding to exotic grasses is due to the change in species, when analysis of experimental data indicates that it is mostly a result of increase in soil nutrient availability due to tillage. These concerns are directed towards unwise decisions to cultivate land that has previously been considered unsuitable for tillage because of the arid climate and erosional problems (both wind and water).

Sufficient research has not been undertaken in Canada to determine whether it is advantageous to replace the native grasses by exotic grasses. Such research results as are available in the Northern Great Plains of Canada and the United States either: (i) do not support claims concerning the magnitude of the productive advantage of the exotic grasses; (ii) can be interpreted to show a disadvantage of exotic grasses; or (iii) have been from experiments that have been biased towards the performance of exotic grasses.

If an exotic legume is developed that can persist in competition with grass, this would change the situation drastically. The continuing supply of nitrogen to the grass would then be assured and the productivity of the system would be permanently increased.

There are serious concerns for the future with respect to the capacity of our croplands to sustain the present levels of production. Fragmentary data that are available suggest that perhaps as much as half of their fertility has been lost since they were first cultivated. Recently we have been advised of increasing salinity in our croplands. Both of these observed evidences of deterioration are apparently accelerated by summerfallowing (to which practice a third of our croplands are assigned each year). Who knows what additional more subtle changes are taking place in cropland soils? It seems necessary to revert to less exploitive procedures to protect the productive capacity that remains. This suggests the need for greater inputs by chemicals to control pests, another area which causes concern for the future health of cropland ecosystems and of organisms dependent on them.

In order that we may be in a position in the future to assess the degree of deterioration in our managed ecosystems, it is essential that we maintain some reference areas in a natural state. If experience shows that management regimes are failing to sustain productivity of croplands and rangelends, such reference areas will be invaluable as a basis for understanding what types of modifications will be advisable in management inputs. Great care must be taken to assure that selected areas are protected on a perpetual basis. Through the Canadian contribution to the International Biological Program candidate areas have been selected and much effort has been expended in arranging for protection. This must continue until success is achieved through the passage and implementation of adequate legislation. Hopefully, management procedures in the proposed Grassland National Park in southern Saskatchewan will be such as to protect some natural grassland in perpetuity against the ravishing effects of agriculture, urbanization, strip mining, road building, and the extraction of petroleum products.

References

Coupland, R.T. 1974. Conservation of grasslands. In Conservation in Canada: a Conspectus. (eds. J.S. Maini and A. Carlisle). Canada Department of the Environment, Canadian Forestry Service, Pub. No. 1340. Ottawa.

Johnston, A. 1970. A history of the rangelands of western Canada. J. Range. Management, 23: 3-8.

Johnston, A. and Smoliak, S. 1977. The potential of Canada's forage crops. Agrologist, 6(2): 10-13.

Mondor, C. 1976. The Canadian plains: the vanishing act. Nature Canada, 5(2): 32-39.

Morton, A.S. and Martin, C. 1938. History of Prairie Settlement and Dominion Lands Policy. Vol. II of Canadian Frontiers of Settlement (eds. W.A. Mackintosh and W.L.G. Joerg). The MacMillan Co. of Canada Ltd., Toronto.

Murchie, R.W. 1936. Agricultural Progress on the Prairie Frontier. Vol. V of Canadian Frontiers of Settlement (eds. W.A. Mackintosh and W.L.G. Joerg). The MacMillan Co. of Canada Ltd., Toronto.

Shields, J.A., Rostad H.P.W. and Clayton, J.S. 1970. Inventory of Saskatchewan Soils and their Capability for Agricultural Use. A.R.D.A. Pub. M13, Sask. Inst. of Pedology, Univ. of Sask., Saskatoon.

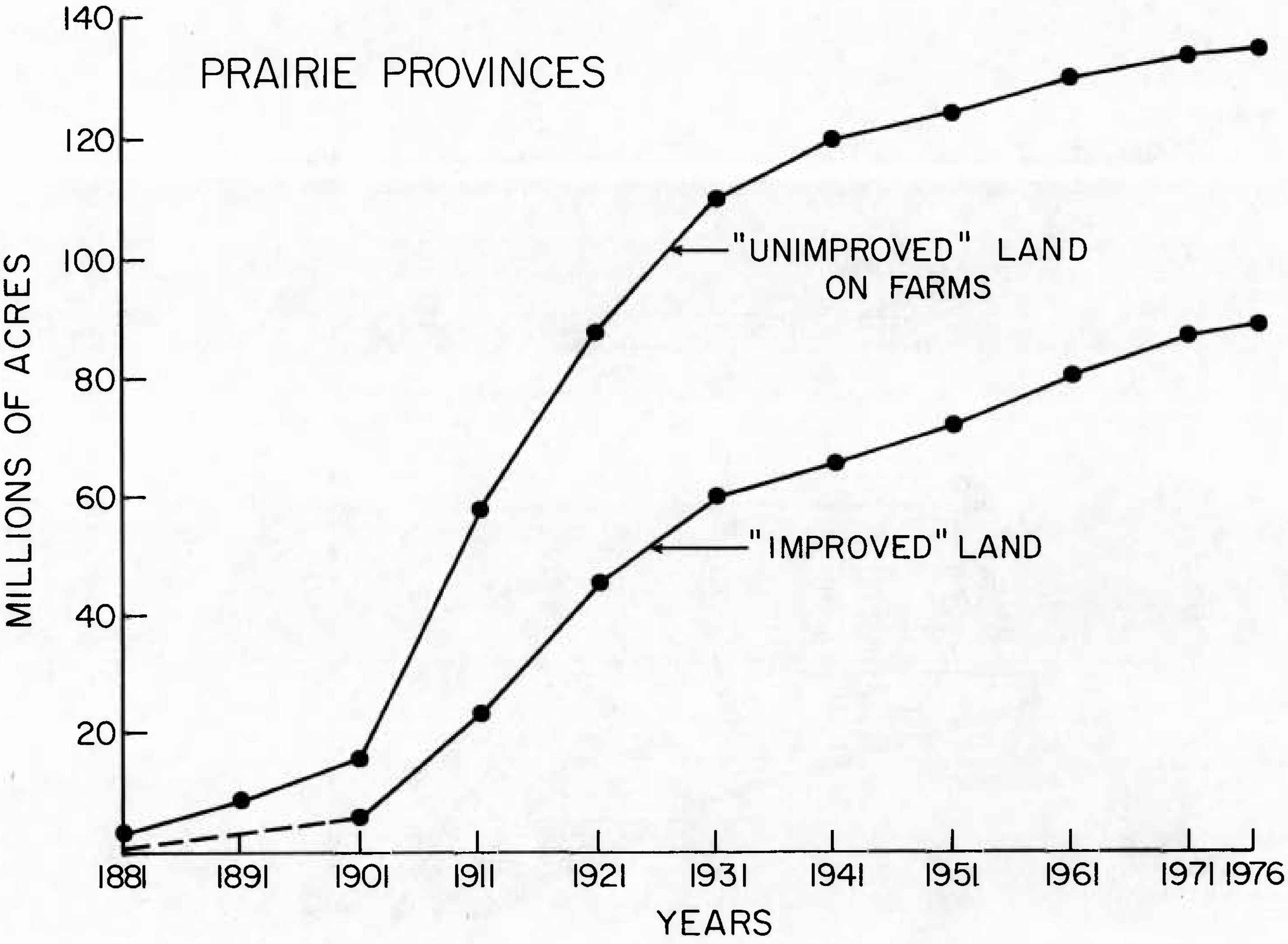

Fig. 1. Increases in area of "improved" land (cultivated land and farmsteads) and in total area of occupied farmland in Manitoba, Saskatchewan and Alberta since the railroads entered the region.

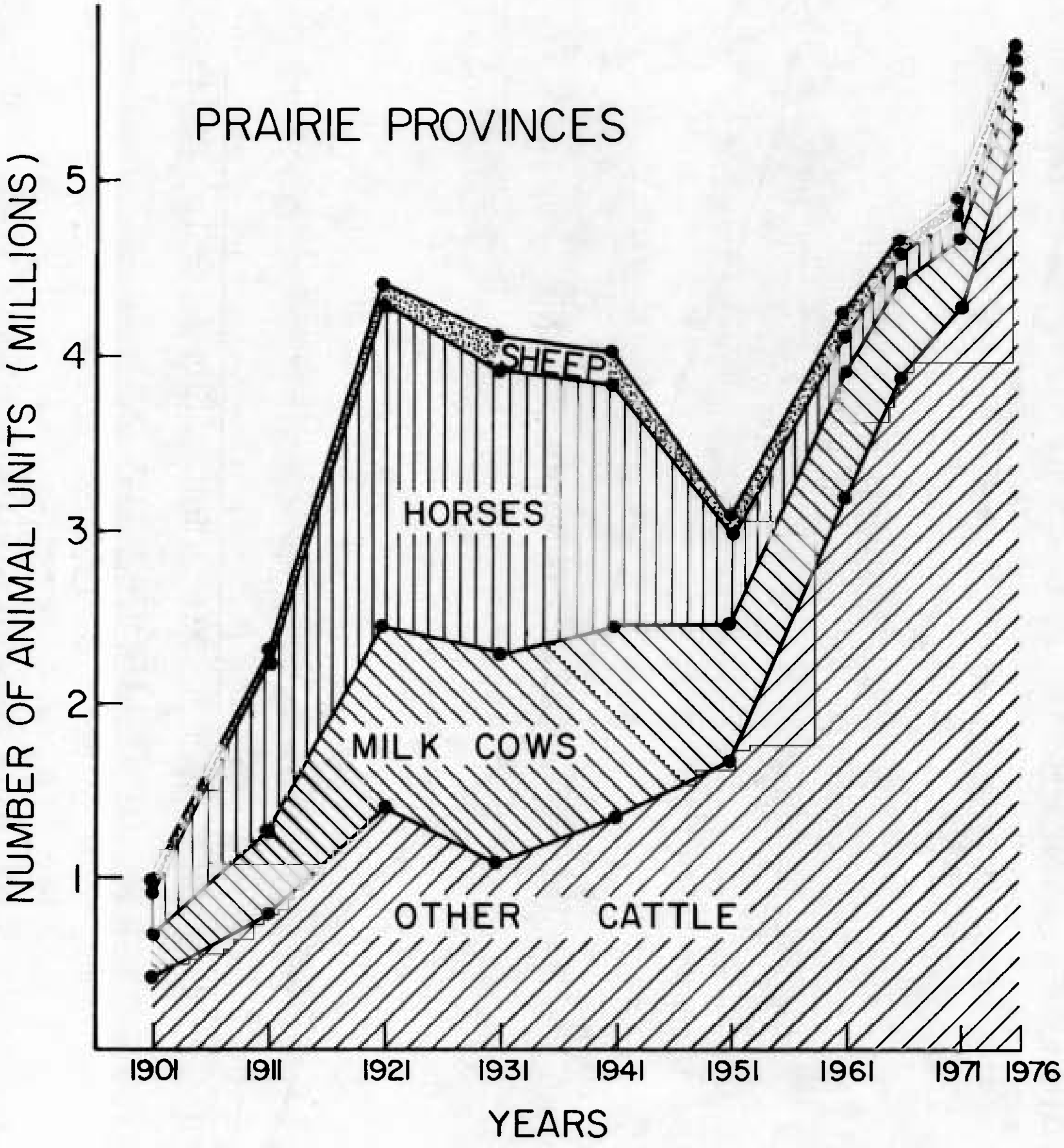

Fig. 2. Changes in the grazing load by livestock in Manitoba, Saskatchewan and Alberta since the period of rapid agricultural settlement began. Each animal unit is the equivalent of 1 milk cow or 1.25 horses (of all ages) or 1.67 "other cattle" (of all ages) or 6.67 sheep (of all ages) at the time census data are taken in June.

ECONOMIC ASPECTS OF THE PRAIRIE PROVINCES

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While the Prairie Provinces have only 16 percent of Canada's total population, the region does have a predominant position in the nation's agricultural industry. Most of the improved farmland (80 percent or 88 million out of a total of 108 million acres), a large proportion of the nation's farmers (40 percent), one-half of Canada's farm production and almost two-thirds of Canada's farm exports originate in the Prairies. There can be little doubt about the importance of the farm industry in Western Canada or its importance to the rest of the country.

While a large part of Canada's agricultural production is located in the Prairies, the majority of the domestic food consumers are located in Central Canada. Six of the ten largest urban centres in Canada are found in Ontario and Quebec; these six urban centres have a population of nearly 7½ million people, almost one-third of Canada's total population.

Equally significant from a political and a farm policy point of view is the fact that 162 parliamentary seats in the Federal Government are located in Ontario and Quebec while only 45 seats are found in the Prairie Provinces.

One cannot really understand the current economic, social and political affairs of the Prairie Provinces without a knowledge of the history of this part of the country. If the Prairie Provinces reflect nothing else, they reflect the historical adjustment of a region to the uncertain and unpredictable forces of nature, the world economy and political events in Ottawa.

The Prairie Provinces were developed in spite of early evidence that the whole region was not hospitable to permanent settlements. In 1857 Captain Palliser headed an expedition to Western Canada. Here, in part, is what he reported as a result of his explorations: (1)

> *"The grass is very short on these plains, and forms no turf, merely consisting of little wiry tufts. Much of the arid country is occupied by tracts of loose sand, which is constantly on the move before the prevailing winds. This district, although there are fertile spots throughout its extent, can never be much advantage to us as a possession. In June and July, the Expedition experienced great inconvenience in traversing it, from want of wood, water and grass."*

The prophetic nature of Captain Palliser's observations would one day be recalled. In the meantime, and in spite of Palliser's warnings, the Prairies were developed and settled as a part of Sir John A. MacDonald's "National Policy". This Policy had two general purposes:

1) settlement of the Prairies as a defence against the possible intrusion of the U.S.A. into the north-west territories.
2) development of a commercial frontier for the benefit of manufacturing and investment interests in Central Canada.

The arid land of which Captain Palliser spoke was not without persistent difficulties -- primarily drought and rust. In 1914, for example, many parts of Saskatchewan and Alberta suffered almost complete crop failure as a result of a widespread drought; 1916 was a year of plant rust; again during the period of 1917-1921 drought pervaded a substantial portion of the semi-arid plains.

Without the introduction of Red Fife wheat (later replaced by Marquis wheat in 1910) and black summerfallow, the twin scourges of drought and rust would have made settlement in the Prairies almost impossible. Even so, farm abandonment in some of the dry areas of Alberta and Saskatchewan began as early as the 1920s.

But the worst was still to come. The 1930s coincided with a decade of unprecedented distress in the Prairies. The most vivid description of this decade in the Prairies may be found in James Gray's book, The Winter Years. Gray described conditions in southern Manitoba and Saskatchewan in 1936 as follows: (2)

> *"The soil blowing across the roads and railway tracks was caught and held by Russian thistle until it drifted to the tops of fences and snow-fences, and all that could be seen was the tops of posts. In southern Alberta, the C.P.R. used snowplows to clear the tracks of soil drifts ten feet high..... Administration set the disaster area at over 60 million acres, of which 45 million acres were once prosperous and occupied farm land...... The year 1938 began with rain and considerable promise.... Then came hail, rust and grasshoppers.... The worst grasshopper blizzard within the memory of man hit Regina on August 11 (1938)."*

But dust and grasshoppers were only the outward signs of distress in the Prairies during the 1930s. The real story was etched in the faces of hungry families, abandoned farm homes and the relief camps. In 1931 the Canadian Red Cross sent out a nation-wide appeal for help for 125,000 destitute farm people in Saskatchewan. Food, clothing and blankets arrived by the carload.

The resourcefulness of Prairie farm people in those dark days of the 1930s was illustrated in many ways. James Gray tells the story of one farm family (not untypical) which did everything possible to maximize the use of water through a form of recycling: bath water (after 2 or 3 children had used the same bath) was poured into a barrel until the dirt settled; the water from the barrel was then used to wash clothes; after the clothes were washed the water was carefully used in the garden.

Many policies and programs were forged out of the experiences of the 1930s.

In 1935 the Federal Government established the Prairie Farm Rehabilitation Administration. This agency had as its primary purpose, the development of major soil and water conservation programs. Its activities included farm dugouts for water, strip farming, community pastures for cattle and major irrigation projects.

In 1935 the Canadian Wheat Board was established to deal with the disastrously low grain prices experienced by farmers during the early 1930s.

In 1939, the Government of Canada established the Prairie Farm Assistance Act. This legislation was designed to provide farmers with a crude form of crop insurance -- whenever crop yields in a township dropped below a certain level, farmers received crop payments from the P.F.A.A.

Within a few years, the distress of the 1930s was gradually forgotten. For the period 1935-39, total net farm income for the Province of Saskatchewan averaged $27 million per year. By 1949 net farm income in Saskatchewan had risen to $357 million and by 1975 it was $1.3 billion.

While the drought and crop failures of the 1930s were soon forgotten during the 1940s and 1950s, the searing heat and widespread drought of 1961 were grim reminders that the Prairie farm economy depends heavily on the weather. The average yield of wheat for the Prairie Provinces in 1961 amounted to 10.6 bushels per acre, about one-half of the yield of the year before. Expressed another way, total wheat production in the Prairies was 238 million bushels less in 1961 as compared to the year before, or a total reduction in wheat production of approximately $450 million.

We have learned much from our past experiences. Farmers know much more about soil management and conservation techniques. Much has been learned about water conservation and management in the Prairies. We have a comprehensive crop insurance program to protect farmers' incomes against the ravages of nature. Farmers' incomes are now better protected through such programs as the Grain Income Stabilization Program.

But the widespread drought in 1961 and the soil drifting which occurred during the winter and early spring of 1977 demonstrated that weather can still have a decisive effect on the Prairies. Whether the Prairies could withstand 3, or 4 or 5 consecutive years of drought remains to be tested.

The Prairie farm region has often been referred to as a "boom and bust" economy. No other region in Canada is as vulnerable to the vagaries of the world market and the weather as the Prairie Provinces. The sudden and unpredictable impact of rust, hail, drought, grasshoppers, bumper wheat crops and booming export sales are reflected in tremendous variations in farm income -- variations which not only have an immediate effect on the farmers themselves but which have serious implications for the whole economy in Canada. For example the average year-to-year variation in net farm income in Saskatchewan for the period 1961 to 1975 was 86 percent compared to only 20 percent for the Province of Ontario. In other words, net farm income in Saskatchewan in any given year can vary, on the average, anywhere from 86 percent below or above the income of the year before. Few other occupations or industries have a variation in income of this magnitude.

Weather aside, by far the most important factor insofar as the economic welfare of the Prairie Provinces is concerned must be the export markets for Canadian farm products. Over one-third of Canada's farm production is exported at the present time: expressed another way, if farm production were geared to domestic food needs only, one-third of Canada's farmers and their resources would be redundant. Not only is the export market of vital concern to the Canadian farmer, but the export earnings from Canadian farm products will become increasingly vital as Canada's export earnings from oil and gas begin to diminish during the next few years.

What does the future hold for the Prairie Provinces? Will there be food surpluses or will there be an unlimited demand for exports from the Prairies? Do the Prairie Provinces have the capacity for substantial increases in production?

No one, of course, can answer these questions with much confidence or certainty. However, I will venture a few general observations about the future outlook for the Prairies.

Events of the past four or five years have indicated that agricultural productivity and abundance should not be taken for granted.

A world food shortage became quite critical in 1972 when drought in several countries led to a reduction in world grain production of 4 percent, a significant drop when compared with the world demand for food which increases at the unrelenting rate of 2 percent per year. In 1973 a major drought in Russia led that country to purchase one-fourth of the wheat crop in the U.S.A. The impact of this purchase caused a violent response in world prices of grain. Continued poor weather in many countries in 1974 coupled with a fertilizer shortage led to what was called the "world food crisis". The world stockpile of grain that in 1961, was equivalent to 95 days of world consumption dropped to less than a 26-day supply in 1974.

Carryover of wheat in the Prairie Provinces plummeted from approximately one billion bushels in 1969-70 to about 300 million bushels in 1974-75, while wheat prices skyrocketed from $1.68 to $4.47 per bushel. During the same period of time in the U.S.A. idle land in the U.S. land bank dropped from about 75 million acres to nearly zero.

Table 1. Total net income of farm operators
from farming operations
Ontario and Saskatchewan

Years	Ontario	Saskatchewan
average	millions of dollars	
1935-39	101	27
1949	346	357
1951	448	532
1956	258	402
1961	307	100
1966	467	566
1967	376	361
1968	417	485
1969	449	452
1970	445	242
1971	366	477
1972	524	408
1973	704	982
1974	792	1,203
1975	804	1,262
Average year-to-year variation 1961-1975	20%	86%

During the World Food Conference in Rome in November, 1974, daily press reports described the threat of widespread famine. The New York Times described the mood of the World Food Conference in this way:(3)

> *"From drought-besieged Africa to the jittery Chicago grain market, from worried government offices in Washington to the partly-filled granaries of teeming India, the long-predicted world food crisis is beginning to take shape as one of the greatest peacetime problems the world has had to face in modern times."*

Now let me cite from a recent international news release dated June 3, 1977, which comments on the wheat situation in the U.S.A.: (4)

> *"Taking production (wheat) and carryover together, the total supply will be about 3.150 billion bushels, up from 2.812 billion bushels last year and 2.137 billion bushels as recently as 1974. This large amount presents a serious disposal problem that will have to be solved by a major crop problem some place in the world, a large feed use, a drastic reduction in acreage, or some combination."*

> *"The reduced U.S. wheat exports this year are the result of very large world grain crops in 1976. Wheat production outside the U.S. was 355 million tons compared to 292 million in 1972 and the previous record of 325 million in 1973. Coarse grain production outside the U.S. was 497 million tons (1976). The previous record was 474 million tons in 1973."*

How does one reconcile the food crisis in 1974 with the impending food surplus problem in 1977?

I believe one commentator at the World Food Conference in 1974 summed up the situation: (5)

> *"Crises have their ups and downs, and before long bumper or even record crops here and there could make the world food crisis seem like an exaggerated peril. But the race between food production and rising population will be far from over. The margin of safety, should one develop, is not likely to grow large again for some years......the condition is chronic, not transient."*

If there is one conclusion that can be drawn from the experience between 1974 and 1977 it is that some form of food reserve seems necessary if the margin between food scarcity and surplus is as precarious as many suggest.

Without some form of reserve, we can expect violent fluctuations in farm prices. The unpredictable swings in world demand and supply can create enormous upward and downward pressures on farm prices in Canada.*

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* For example, in 1975, Soviet grain output was 140 million tons; in 1976, the grain harvest amounted to an estimated 220 million tons - a difference of 80 million tons or close to 3 billion bushels. The impact on the Canadian farm industry of swings of this magnitude can be enormous.

Dr. Lester Brown has expressed the importance of a food reserve in the following way: (6)

> *"Since 1960, world grain reserves have fluctuated from a high of 155 million metric tons to a low of about 100 million tons. When these reserves drop to 100 million tons, severe shortages and strong upward price pressures develop. Although 100 million tons appears to be an enormous quantity of grain, it represents a mere 8 percent of annual grain consumption, or less than one month's needs - an uncomfortably small working reserve and a perilously thin buffer against the vagaries of weather and plant diseases."*

The responsibility for this food reserve must not only be international in scope but its cost must be borne by food importing as well as exporting nations. Farmers in the Prairie Provinces support the idea of a food reserve providing that it is not at their direct expense such as happened with the cummulated food surpluses of the 1950s and the 1960s.

In my opinion, farmers have the capacity (weather co-operating) in the relatively short-run to supply the commercial needs of the domestic and international markets. Indeed, it is almost certain that troublesome surpluses in some commodities will appear once again.

But I do not regard it as prudent to develop long-run farm policies on the basis of scarcity and production constraints. During the past two decades increased food production has depended more on biological and technological innovations than on increased land supply. I believe that the more developed countries are already operating near the limits of presently available technology. The evidence would appear to suggest that the margin of safety in food production is becoming increasingly narrow.

While world population continues to increase at 75 million people per year, the capacity to increase food production is becoming more difficult and more costly.

A recent report by the National Academy of Sciences in the U.S. concludes that: (7)

> *"Professional analysts and planners have a disturbing habit of assuming that new technologies and practices will be automatically forthcoming....Long range planning based on continued linear upward projections of productivity of all parts of agriculture can be hazardous.....the biological realities suggest a slowing of the rate of increase in productivity for most crops in the forseeable future..."*

The increase in oil prices, and the corresponding impact on the price of commerical fertilizers, adds further to the difficulty of increasing food production.

New and dramatic breakthroughs in agricultural research will be required if the margin of safety is to be widened -- new breakthroughs of the magnitude and importance of such innovations of the past quarter century as hybrid corn, chemical fertilizers, insecticides and herbicides. Whether these breakthroughs occur in photosynthesis, growth stimulants or new genetic species remains to be seen. The essential thing is that fundamental research must be stressed if the limits of known technology are to be broken.

In the long-run there can be little doubt about the growing demand for food. The land/man ratio is growing -- between 1960 and 1975 the number of persons per square kilometre of world land area increased from 22 to 29, an increase of over 30 percent. The land/man ratio during the same period increased by only 20 percent in North America compared to 50 percent in South Asia (table 2).

Agricultural population per square kilometre of agricultural land shows an even greater discrepancy between the developed and underdeveloped regions of the world varying from a figure of 5 for North America to a high of 453 for East Asia (table 3).

What is worse, the rate of population growth is greatest in those areas and regions with the greatest population density at the present time (table 4). The rate of natural increase in population growth varies from 7.2 per 1000 population in North America to 25.9 per 1000 population in South Asia.

What the eventual population growth will be is almost anyone's guess. However, recent estimates suggest that world population by the year 2000 could be 6.4 billion and by the year 2025 close to 9.1 billion people (table 5). How much of the food supply will be produced in those regions with the greatest population growth is difficult to estimate but there can be little doubt that a population increase of the magnitude now being projected will have an enormous impact on the Prairie Provinces over the next 25 years.

In summary, it is my opinion that the economic prospect for the Prairies in the short-run will continue to be one of unpredictable fluctuations in yield, prices and incomes. This instability will be felt, not only by the farmers themselves, but by the rest of the country. During the past ten years wheat exports have varied from 300 million to 500 million bushels, most of which variation has been due to the year-by-year changes in demand for Canadian wheat by Russia and China. A difference of 200 million bushels in wheat exports means a loss (or gain) in export earnings of close to a half-billion dollars and a corresponding loss (or gain) in domestic purchasing powers.

In the longer run, it would appear that the Prairie Provinces will be called on to produce at greater capacity. In a decade from now, approximately 800 million people will be added to the world's population. It is highly likely that a significant proportion of the food supply for this increase in population will have to come from the Prairies.

It could very well be the case that increased food production could be one of the greatest peace-time challenges the world has had to face in modern times.

The arid plains described by Captain Palliser in 1857 could be, in fact is, one of the most important renewable resources possessed by Canada. To manage and conserve this resource for the benefit of this and succeeding generations is an awesome responsibility indeed. But it is a responsibility we cannot evade.

References

1. Report of the Royal Commission on the South Saskatchewan River Project, Chapter 3. Queen's Printer, Ottawa, 1952.
2. Gray, J.H. The Winter Years. MacMillan of Canada, Toronto, 1966.
3. A Report on the World Food Crisis; Give Us This Day.... Staff of the New York Times. Arno Press, New York. 1975.
4. United States Department of Agriculture. Foreign Agriculture. June, 1977.
5. A Report on the World Food Crisis; Give Us This Day.... Staff of the New York Times. Arno Press, New York, 1975.
6. Brown, L.R. and Eckholm, E.P. "Food and Hunger - the Balance Sheet". Challenge, September/October, 1974, New York.
7. National Academy of Sciences, Agricultural Production Efficiency. Washington, D.C. 1975.

Table 2. Land area, population density in 1960 and 1975, and 1960–1975 gain in population density, in the world and major areas

	Land area (thousand km^2)	Inhabitants per km^2		Gain in density, 1960–1975
		1960	1975	
World total	135,779[a]	22.1	29.4	7.3
More developed regions	60,907	16.0	18.6	2.6
Less developed regions	74,872	27.0	39.5	12.5
Europe	4,936	86.1	96.0	9.9
USSR	22,402	9.6	11.4	1.8
Northern America	21,515	9.2	11.0	1.8
Oceania	8,509	1.9	2.5	0.6
South Asia	15,775	54.9	80.4	25.5
East Asia	11,756	67.0	85.5	18.5
Africa	30,320	9.0	13.2	4.2
Latin America	20,568	10.5	15.8	5.3

[a] Not including the Antarctic continent.

Table 3. Agricultural population, agricultural land area, and agricultural density, 1950 and 1970, in the world and major areas

Area	Agricultural population (millions)		Agricultural land area (thousand km^2)		Agricultural population per km^2 of agricultural land	
	1950	1970	1950	1970	1950	1970
World total	1,580	1,862	12,290	14,010	129	132
More developed regions	299	206	6,500	6,690	46	31
Less developed regions	1,281	1,656	5,790	7,320	221	226
Europe	128	89	1,470	1,480	87	60
USSR	101	77	2,250	2,330	45	33
Northern America ...	22	10	2,210	2,200	10	5
Oceania	4	4	190	240	19	18
South Asia	545	763	2,400	3,250	227	235
East Asia	523	561	1,060	1,240	493	453
Africa	171	239	1,870	2,040	92	117
Latin America	87	118	840	1,230	104	96

Table 4. Birth rates, death rates and rates of natural increase, 1960-1970 and 1970-1975, in the world and major areas (rates per 1,000 population)

	Birth rate		Death rate		Rate of natural increase	
Area	1960-1970	1970-1975	1960-1970	1970-1975	1960-1970	1970-1975
World total	33.3	31.8	14.1	12.8	19.2	19.0
More developed regions	19.3	17.2	9.1	9.2	10.2	8.0
Less developed regions	39.2	37.8	16.6	14.4	22.6	23.4
Europe	18.1	16.1	10.2	10.4	7.9	5.7
USSR	19.8	17.8	7.7	7.9	12.1	9.9
Northern America	21.0	16.5	9.3	9.3	11.7	7.2
Oceania	25.4	24.7	10.3	9.4	15.1	15.3
South Asia	44.6	42.7	19.8	16.8	24.8	25.9
East Asia	28.7	26.0	11.5	9.8	17.2	16.2
Africa	47.0	46.5	22.1	20.0	24.9	26.5
Latin America	38.6	36.7	10.5	9.2	28.1	27.5

Table 5. Population of the world and eight major areas, at 25-year intervals, 1925-2075 (millions)

Major Area	1925	1950	1975	2000	2025	2050	2075
World total	1,960	2,505	3,988	6,406	9,065	11,163	12,210
Northern group	1,203	1,411	1,971	2,530	2,930	3,084	3,107
Northern America	125	166	237	296	332	339	340
Europe	339	392	474	540	580	592	592
USSR	168	180	255	321	368	393	400
East Asia	571	673	1,005	1,373	1,650	1,760	1,775
Southern group	757	1,094	2,017	3,876	6,135	8,079	9,103
Latin America	98	164	326	625	961	1,202	1,297
Africa	153	219	402	834	1,479	2,112	2,522
South Asia	497	698	1,268	2,384	3,651	4,715	5,232
Oceania	9	13	21	33	44	50	52