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NL-339 (r. 88/04)

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BIOGEOGRAPHICAL STUDY OF THE GENUS DRYAS IN THE KLUANE LAKE AREA, SOUTHWESTERN YUKON TERRITORY, CANADA.

by

Alain Pierre Roy

A thesis
presented to the University of Ottawa
in fulfillment of the
thesis requirement for the degree of
Master of Arts
in
Geography

ISBN 0-315-46850-5

UNIVERSITÉ D'OTTAWA
UNIVERSITY OF OTTAWA

ABSTRACT

The primary objective of this research was to determine the regional distribution of each major type of *Dryas* identified in the Ruby and Kluane Ranges of southwestern Yukon. This objective implied the necessity to develop an appropriate regional typology since the existing identification schemes have serious limitations which could have created artificial results. Two scales of the landscape were examined: regional and local. This study was also concerned with the implications of space in the structure of the distribution.

From the typology, nine types were recognized, of which six are distinct species or ecotypes. These types were then compared with a traditional North American taxonomical treatment. Most types do fit a species definition, but the taxonomy does not record the importance of hybridization. This is the main advantage of the typology: it allows the study of the genetic interactions through phenotypic variation.

All major types of *Dryas* were found to hybridize when populations were in close proximity. Distance seems to be the only barrier to hybridization.

The PEGASE procedure produced two models of explanation of the distribution pattern. The first one is mostly chorological, while the second identifies a number of regional variables as the best descriptors of the pattern when the chorological variables are eliminated. Careful interpretation of the real ecological meaning of the variables of the second model is necessary since most ecological variables are inherently chorological because of their imprecision and their own regional pattern of distribution. In both models however, relative altitude was identified as the local factor which best accounted for the altitudinal stratification of types in one particular massif of the Kluane Ranges.

A hypothetical regional model has been postulated to account for the distribution of the species at that scale. It contends that the observed pattern of distribution of the *Dryas* species reflects the evolution which has taken place in the landscape since dispersal patterns and initial site conditions resulted for a given site in the exclusive establishment of a *Dryas* species or its dominance over other ones, at the time of colonization or later through competition and resource partitioning.

RÉSUMÉ

L'objectif principal de cette recherche a été l'étude de la distribution régionale des principaux types de *Dryas* identifiés dans les chaînes Ruby et Kluane du sud-ouest du Yukon. Cet objectif impliquait la nécessité de développer une typologie régionale appropriée, étant donné que les classifications taxonomiques courantes auraient pu donner des résultats artificiels. Deux échelles du paysage ont été examinées, les échelles régionale et locale. Cette recherche portait aussi sur les implications de l'espace dans la structure de la distribution.

A l'aide de la typologie, neuf types ont pu être reconnus, six desquels sont des espèces distinctes ou des écotypes. Ces types ont été mis en parallèle avec un traitement taxonomique traditionel. La plupart des types correspondent à une espèce déjà reconnue, mais la taxonomie ne tient pas compte de l'hybridation. C'est là l'avantage principal de la typologie: elle permet l'étude des intéractions génétiques par l'entremise de la variation phénotypique.

Tous les principaux types de *Dryas* peuvent se croiser et produire des populations hybrides viables lorsque les espèces parentales sont voisines. L'éloignement semble être la seule barrière au croisement de deux populations.

La méthode PEGASE a produit deux modèles explicatifs du patron de distribution. Le premier est surtout chorologique alors que le second identifie les variables écologiques qui expliquent le mieux la structure de la distribution lorsque les variables chorologiques sont éliminées. La prudence est de mise dans l'interprétation des variables du second modèle car celles-ci ont le plus souvent un caractère chorologique caché dû à leur imprécision et à leur

propre patron régional de distribution. Par contre, les deux modèles retiennent l'altitude relative comme le meilleur descripteur de la stratification altitudinale des espèces présentes dans un des massifs de la chaîne Kluane.

Un modèle hypothétique est présenté dans une tentative d'explication du patron à l'échelle régionale. Selon ce modèle, le patron de distribution observé est l'expression de l'évolution qui s'est produite dans le paysage depuis que, selon le site, établissement exclusif ou dominance d'une espèce particulière de *Dryas* résultait des possibilités de dispersion et des conditions initiales du milieu, lors de la colonisation ou plus tard, suite à des effets de compétition ou de compartimentage des ressources.

ACKNOWLEDGEMENTS

I would like to extend my gratitude to the following people who have helped me along this exercise:

to M.A. Geurts for letting me use a wonderful microscope without which the morphological analysis would undoubtedly have been much more painful;

to D. Lagarec, for a much appreciated "layman's interest" in the subject, and thought-provoking comments and questions on several aspects of this research;

to A. Langlois, for formally introducing me to multivariate methods, and for helpful comments on specific methods;

to P. Johnson, for making this study possible by providing me with the chance to visit areas of both ranges which would have been unaccessible otherwise;

to family and friends, for putting up with me all along;

and last but not least, to my supervisor, M. Phipps, for the time he has invested in this study, as well as the patience and interest he has shown throughout.

I would like to acknowledge the cooperation of the Yukon Territorial Government and Parks Canada who granted me the permits required for the collection of specimens in the field. This research was made possible by grants from Indian and Northern Affairs through the Northern Training Grants program.

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Chapter I

INTRODUCTION

This study will focus on the distribution of the alpine members of the genus *Dryas* (*Rosaceae* family) in the southwestern region of the Yukon Territory. There is much evidence of geographic variation of this genus and its yet unresolved taxonomical interpretation has caused much controversy. Some authors believe that the contact of different members of the genus commonly results in hybrid swarms (Hultén 1959, Elkington 1965) while others believe that important hybridization is a less frequent and very localized phenomenon (Porsild 1947, Porsild and Cody 1979). This thesis will attempt to address the problem from a geographical perspective by examining the geographic variation of the genus and determining the general characteristics as well as the distribution of the major types which will have been identified. The ecology of their individual distribution pattern will then be studied.

Dryas is, superficially at least, a relatively well known genus of the *Rosaceae*. Most of its notoriety probably stems from its circumboreal distribution and generally important contribution to primary productivity where it is found. Its commonness in arctic and alpine environments may be at the origin of the feeling of apparent adequacy of knowledge concerning the genus. In fact, nothing could be further from the truth. In the 1940's and 50's, two botanists studied the genus and produced conflicting taxonomical classifications, a demonstration of the complexity of the genus (Porsild 1947, Hultén 1959). It has taken until very recently for a study to explore some of the basic relationships which exist between some of the members of the genus (McGraw and Antonovics 1983).

The question at the origin of this thesis was an indirect result of a 1984 ecological survey in the north-central Ruby Range. After comparing our results with those already published for the southwestern Yukon region, it appeared that two species shared the regional alpine ecosystem: *Dryas octopetala* L. and *Dryas integrifolia* M. Vahl. Our survey indicated that only *D. octopetala* was present in the north-central sector of the Ruby Range. A similar study done in the south-central sector (Price 1971) had given the same result. It seemed that *D. integrifolia* was probably confined to the Kluane Ranges. The possibility of a regional segregation pattern was now apparent. None of the botanical and ecological studies done so far in the region, nor their combination could provide more than a partial and totally inadequate answer.

Ecological studies, while adhering generally to a rigorous sampling scheme, are most times too site-specific and cannot afford to be critical of the taxonomical treatment for a particular genus. Botanical studies, on the other hand, contain much information about the taxonomy of the genus but all too often have a sporadic distribution which makes them less valuable when environmental factors are to be examined. Thus, in spite of an apparently good knowledge of the genus (a fact which may be truer as far as the general worldwide distribution is concerned), little could be said with much certainty about the biogeography of the genus *Dryas* in southwestern Yukon. Therefore, in a regional study of the geography of this genus, the first step would be to determine approximately the extent of the distribution of the two more important species reported — *D. octopetala* and *D. integrifolia* as well as the less common ones— to get an idea of the nature of their respective distribution.

This step quickly created a further problem, namely that of the identification of the specimens collected since many of them could not be identified properly using the existing classification schemes. In all too many cases the morphological differences observed could not be equated to taxonomical distinctions mentioned in the literature. Thus the need to develop a typology of the genus adapted to the study area. It should be clear from the outset that a regional typology of the *Dryas* is by no means equivalent to a taxonomy of this same genus since the former does not attempt to develop a hierarchy of the types found but only to circumscribe them for identification purposes using a number of morphological characters deemed of importance.

Given the extent of the area to be examined, the study would have to be limited in scope in order to make it feasible within the limits imposed by the degree and the resources available. Accordingly, the emphasis would be on the study of the regional pattern. The local pattern would be studied only to the extent allowed by remaining time and resources, with priority given to the scale of the meso-landscape over that of the micro-landscape. Three scales of the pattern could thus be examined, with decreasing priority: the regional pattern, the meso-landscape pattern and the micro-landscape pattern.

The scope of this study makes it, by definition, classically biogeographical (Pielou 1979, Pianka 1978). Like many other branches of geography, biogeography is often not associated with the discipline best equipped to deal with the central question of distribution in space, namely geography, rather than the discipline associated with the objects referred to in the question, in this case biology or more precisely, botany. A biogeographical study is an interdisciplinary endeavor but as the name implies, the central preoccupation is geographical. This central theme of distribution in space should enable geographers to make important contributions to biogeography.

Chapter II

DESCRIPTION OF THE STUDY AREA: PHYSIOGRAPHY, GEOLOGY AND CLIMATE.

2.1 Geographical Limits

The study area is located in the southwestern corner of the Yukon Territory and comprises the Ruby Range and most of the Kluane Ranges. Its center is at approximately at a latitude of 61 deg 10' N and a longitude of 138 deg 30' W. It is bounded to the east by the Aishihik Lake and River, to the west by the Donjek River, and surrounds Kluane Lake. The study area is roughly rectangular, its northwest-southeast axis being approximately 180km long, while the short axis is 80 to 100km in length (fig. 1).

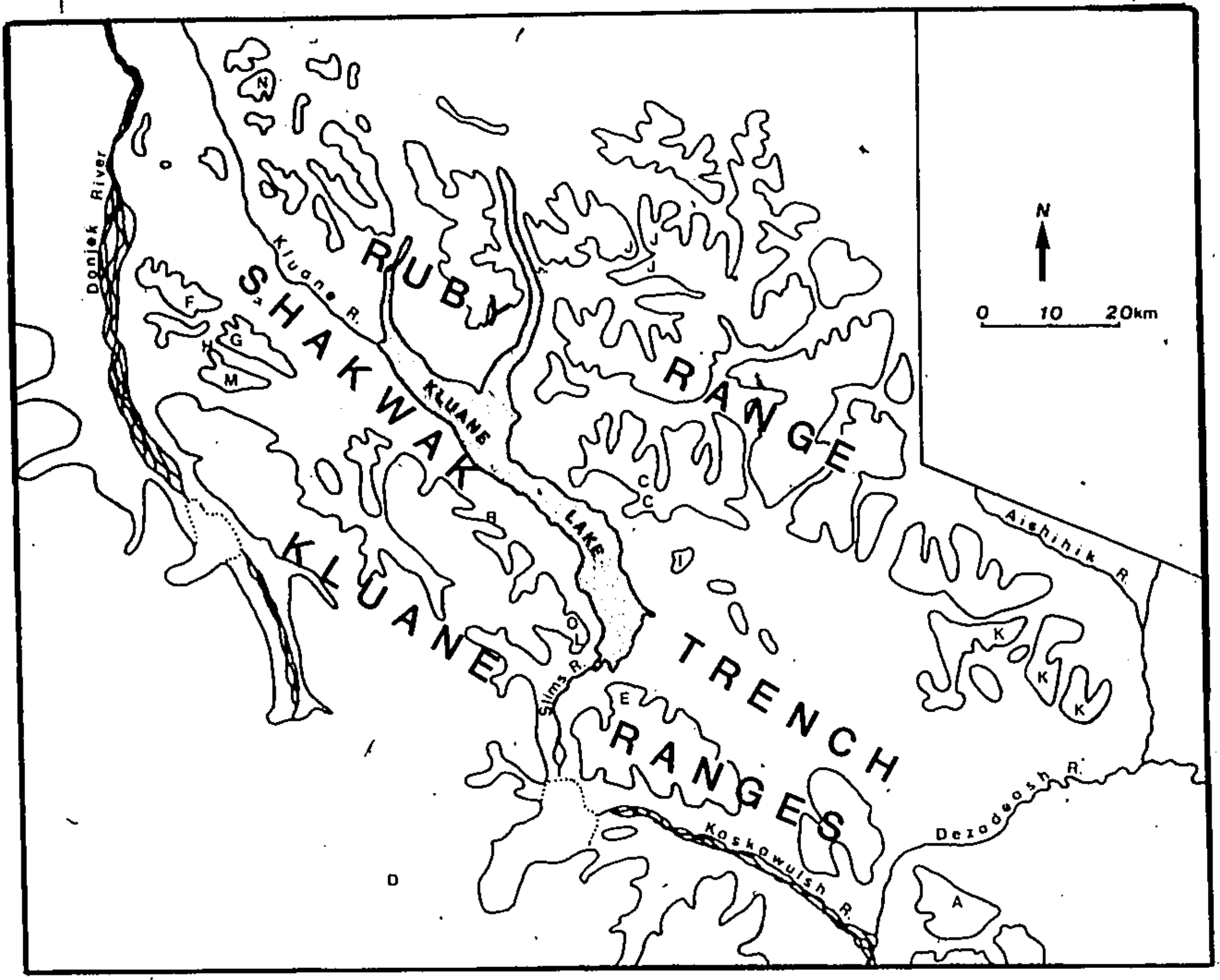


Figure 1: General Geographical Features of the Study Area. Contour lines for area above 5000'. Letters represent sampling locations: A-Auriol massif; B-Bock's Creek; C-Cultus Creek; D-Kaskawulsh; E-Outpost Meadows; F-Nickel Creek; G-Quill Creek North; H-Quill Creek South; I-Ruby Hills; J-Ruby Range North; K-Ruby Range South; L-Sheep Mountain; M-Tatamagouche Creek; N-Tincup Lake; O-Williscroft Creek.

2.2 Physiography and Geology

The Shakwak Valley is a dividing feature of the study area. It is a trench 5 to 15km wide which forms a sharp boundary between the Ruby Range to the northeast and the Kluane Ranges to the southwest. Its central portion is occupied by Kluane Lake, a body of water as much as 80km long but no more than 10km across. The valley floor ranges in elevation from about 600m at either end to roughly 1100m a few kilometers southeast of Kluane Lake.

The Ruby Range forms a part of the Yukon Plateau. Few of its peaks reach 2200m: most of the summits have elevations ranging from 1600 to 2000m. An important batholith of granodiorite, quartz monzonite and quartz diorite constitutes the central portion of the range (Muller 1967). Muller reports that: "To the southwest these granitic rocks are fringed with quartz-biotite schist and gneiss occurring in a belt stretching from south of Gladstone Creek to north of Kluane Lake." This is in general agreement with the report of Templeman-Kluit (1974), although the eastern portion of the belt is often quite tenuous. Just south of the southern portion of this belt lies a "uniformly north-dipping sequence of chlorite-sericite schist"(Muller 1967). The northwest extremity of the range is occupied by an assemblage of metamorphic rocks characterized by bands of recrystallized limestone, quartz-muscovite schist, epidote-amphibolite and some metamorphosed ultrabasic rocks. This geological formation is the only one of the Ruby Range containing an important proportion of limestone.

Across the Shakwak Valley, the Kluane Ranges have summits reaching well in excess of 2600m. There is however a large proportion of alpine habitat comprised between 1600m and 2200m, with several sections of rolling mountains or less severe relief. The geology of the Kluane Ranges is much more complex than that of the Ruby Range, with anything from igneous and volcanic rocks to only slightly metamorphized sedimentary rocks.

In the northwest sector, volcanic rocks are common: propylitic basic lava, banded tuff, volcanic breccia, basalt and andesite. Several metamorphic rocks and sedimentary rocks are also present: chlorite schist, greywacke, argilite, sandstone, limestone, conglomerate, and chert. Lastly, this sector also has an important area of granitic rocks similar to that of the Ruby batholith. The central portion of the Kluane Ranges is certainly the most complex although one can again recognize the predominence of metamorphic and volcanic rocks. All the rock types mentioned for the northwest sector are present as well as several less important metamorphic and volcanic types. The southeastern sector again has several types of rocks but the categories are more clearly segretated. Conglomerate, shale, sandstone, tuff, argilite, chert and greywacke constitute the bulk of the range in that sector. Volcanic rocks are relegated to a secondary place and igneous rocks are all but non-existent (Muller 1967, Kindle 1952, Wheeler 1963).

As Campbell and Rampton (1980) put it: Much of the present topography of the St. Elias Mountains and of the Shakwak Trench was shaped by erosion and by the scour of moving ice during the two more recent Pleistocene glaciations, between 100,000 and 12,500 years ago, and later by erosion, which still goes on.

Muller (1967) states that most of the area under study was at some time covered with ice during the Pleistocene epoch, and that many parts were glaciated several times. He describes three subsequent glaciation events: the Nisling ice sheet (the oldest), the Ruby ice sheet, and the St-Elias advance (the most recent). The Nisling ice sheet is probably pre-Wisconsin (Muller 1967). Projections by Muller (1967) place the average ice level during the glaciation by the Nisling ice sheet at 6000 feet over the northeast sector of the St. Elias Mountains of which the Kluane Ranges form the northern front, and at an average of 5000 feet for the Yukon Plateau, of which the Ruby Range is the southern limit. Local levels can be much higher: Muller attributes erratics found at 7200 feet on Outpost Mountain in the Kluane Ranges (just south of Kluane Lake) to the activity of the Nisling ice sheet. For the Ruby ice sheet, the projections are generally 500 to 1000 feet lower. The St. Elias advance altitudinal limits were generally much lower still. Campbell and Rampton (1980) date the beginning of the period of major continental glaciation at roughly three million years ago, although glaciation probably occured much earlier in the St. Elias. Sedimentary deposits scattered in the Shakwak Trench and Duke Depression have provided evidence of glaciations dating back more than 100,000 years. Rampton (1981) reports that the region has been subjected to repeated glacial and non-glacial intervals since the late Tertiary. There is still a lot of uncertainty concerning the number of Pleistocene glaciations and their dating (Denton and Stuiver 1967, Hughes et al. 1969, Rampton 1981), but deglaciation is generally thought to have been well underway by 12,500 years B.P. (Rampton 1981). "Renewed climatic deterioration marking the beginning of the Neoglaciation (...) occurred around 2800 years ago" (Rampton 1981). The other important and relatively recent events for the region have been two volcanic episodes which occurred in nearby Alaska. Each time, a layer of ash covered most if not all of the study area . The older episode is dated at about 1885 years B.P. and the more recent one at about 1225 years B.P. (Rampton 1981). These layers of ash, now buried, can be found quite commonly throughout the region.

2.3 Climate

The climate of southwestern Yukon is not very well known. The few meteorological stations in the region have not been operating long enough to provide an official climatic norm (Environment Canada 1982), but they contribute to typify the weather. The regional physiography is such that, in spite of the proximity of the Pacific Ocean, the area has a relatively continental climate (Kendrew and Kerr 1955). This is the result of the barrier created by the St. Elias Mountains which effectively shield the study area from direct oceanic influences. The air masses from the Pacific are subjected to complex modifications with the resulting continentality of the climate north of the divide (Taylor-Barge 1969). Kendrew and Kerr (1955) also state that the deep river-valleys which cut through the mountain barrier are "too narrow and tortuous to form atmospheric corridors". As stated by Muller (1967), "the other important factor is the latitude, where long winters, with periods of daylight shortening to less than six hours, contrast strongly with the short summer, when the sun is above the horizon for a maximum of more than 19 hours". The climate is thus continental and subarctic.

There is a seasonal pattern to the importance of the major air masses (Lagarec and Geurts 1984). During the summer, low-pressure systems from Alaska often cross into central Yukon (McKay, Findlay and Thompson 1970). Their influence is clearly felt in southwestern Yukon as indicated by the meteorological records for that region, especially those of Snag and Burwash. In winter, the influence of the Yukon-Mackenzie air mass is felt as far south as the Kluane Lake area. The increased importance of anticyclonic systems explains the typically low winter temperatures (Barry 1981). The St. Elias Mountains are therefore a probably more effective climatic barrier in winter than in summer (Taylor-Barge 1969, Barry 1981).

Within the study area, there is clearly a pattern of precipitations with the central area being the driest. Unfortunately, the low number of stations prevents the partitioning of the region on that basis.

Chapter III

THE GENUS DRYAS: LITERATURE REVIEW

Over the years, the genus *Dryas* has attracted the attention of several scientists, either because it represents an interesting taxonomical problem or simply because its ubiquity in alpine and arctic environments gives it a certain importance in ecological studies, especially those dealing with primary productivity. In this chapter, we will examine the scientific literature relevant to three aspects of this thesis:

1-Taxonomical studies relevant to the elaboration of a sound identification procedure;

2- Botanical studies concerning the life habits and floral biology of the genus which may contribute to a better understanding of the factors involved in the formation of distinct local populations or demes;

3- Studies of the ecology of the genus throughout the world which can contribute to the explanation of its regional ecology, as well as phytogeographical and ecological studies undertaken in southwestern Yukon which may provide some clues concerning the distribution pattern.

3.1 Taxonomical Treatment and the Problem of Identification

A quick examination of the genus *Dryas* in southwestern Yukon is sufficient to recognize three types of Dryas: *D. Drummondii,* which is a very distinct lowland species and two alpine species: *D. octopetala* and *D. integrifolia,* the former with crenate leaf margins, the latter with entire ones. Upon closer examination, however, the assigning of a specimen to one of the aforementioned categories becomes truly problematic. We will therefore review the taxonomical work which has been done so far on this question.

The morphological variations of the genus *Dryas* have been described and studied by several authors of which the more recent are Jessen (1921) for the Arctic, Juzepczuk (1941) for Eurasia, Porsild (1947) for North America, Hultén (1959) for the circumpolar zone and the alpine habitat, Elkington for Greenland (1965) and Great-Britain (1971), and finally, McGraw and Antonovics (1983) for an alpine site in Alaska.

Jessen (1921), in his description of *Dryas octopetala* L. and *D. integrifolia* Vahl, already recognizes that little morphological distinction separates the two species. He in fact includes the sketch of a specimen which he describes as intermediate in gross morphology between *D. octopetala* and *D. integrifolia*. The presence of glandular and branched hairs on *octopetala* leaves as well as the raised lower midvein are mentioned. The revolute leaf margin is interpreted as a reversible response to drought whereas both Porsild (1947) and Hultén (1959) use this characteristic as a classification criterion.

Elkington's detailed study (1965) of the geographic variation of *Dryas* in Greenland points out the usefulness of specific leaf characters for the differentiation of the various species: presence of glands or branched hairs on the median vein and type of margin. According to the same author, the other leaf characteristics are less useful for identification. In Greenland, Elkington found specimens which correspond to *D. integrifolia* Vahl on the western and southeastern coasts. He reports *D.integrifolia*, *D. octopetala* and non-stabilized intermediate forms for the eastern, northern and northwestern coastal sectors. All the mixed populations apparently also contain intermediate forms which have the characteristics expected in the case of an introgressive hybridation between *D. octopetala* and *D. integrifolia*. Elkington considers that the variation patterns described by Hultén (1959) for Alaska and the Yukon are similar to those which he studied.

The various morphological types or phenotypes of the genus have been categorized in two distinct ways. According to the first school, represented by Juzepczuk (1941) and Porsild (1947), the three species commonly recognized, namely *D. Drummondii, D. octopetala* and *D. integrifolia*, can be subdivided in species with better defined attributes. Juzepczuk (1929, in Porsild 1947) states that there are, in the mountains of Asia, several species of *D. octopetala sensu lato.*

In a thorough study of the North American collections, Porsild (1947) also argues in favor of a redivision of the genus in species with more precise characteristics. The argument is based largely on an apparent absence of recognizable crosses producing hybrids, the attributes of which are intermediate to those of the parental species. Porsild thus considers that only the presence or the absence of various glands and hairs on the leaves are criteria for the differentiation of species other than *D. Drummondii*. The degree of leaf pubescence, their shape and size, peduncle and sepal characteristics are not considered to show enough constancy to allow a complete differentiation on their basis. Furthermore, Porsild states that the various phenotypes have generally well defined geographical distributions. The sectors occupied by the various species are said to overlap somewhat locally, but to show little or no phenotypic gradation where species come in contact. Consequently, Porsild treats the various morphological types as distinct species.

In North America, the *Nothodryas* section is represented by *D. Drummondii* Richards which is differentiated from the other North American members of the genus by attributes such as a flattened receptacle, hairy filaments and yellow petals. The *Eudryas* section comprises those members commonly assigned to *D. octopetala sensu lato* and *D. integrifolia s.l.*: the receptacle is convex, the petals are white and the filaments glabrous, the peduncles have one relict bract at most and the leaf base is truncate or cordate (Porsild 1947).

D. octopetala sensu stricto is the sole member of the sub-section *Chamaedrifoliae* of the section *Eudryas* in North America: the median vein of the leaf bears branched hairs. The sub-section *Punctatae* is composed of the following North-American species: *D. punc-*

tata Juz., *D. alaskensis* Porsild, *D. Hookeriana* Juz. The upper surface of the leaves is either covered by sessile glands which are often found on the petioles and stipules, or is simply glandular-viscid along the leaf folds because of a clear secretion. According to Porsild, *D. integrifolia* M. Vahl is an aggressive species of the *Tenellae* sub-section which also includes *D. crenulata* Juz., *D. Chamissonis* Juz. and *D. sylvatica* (Hult.) Pors. in North America. This latter sub-section is characterized by glandless, relatively inconspicuous lower midvein as well as by entire leaf margins, at least in the upper half in the case of *D. integrifolia* and *D. sylvatica*, and by somewhat crenate leaves in the case of *D. crenulata* and *D. Chamissonis*.

In the second approach, supported by Hultén (1959) and Elkington (1965, 1971), the status of species is granted to only three main morphological types: *D. Drummondii* Richards, *D. octopetala* L. and *D. integrifolia* Vahl. *D. Drummondii* Richards is clearly different from the two other types since it is the only one to produce yellow flowers exclusively, the other two producing generally white flowers, with rare exceptions. It is also a lowland species. *D. integrifolia* M. Vahl is distinguished from *D. octopetala* L. by the entire leaf margins, at least in the upper half, and the absence of glands and "octopetala scales" (Hultén, 1959). The leaf margin of *D. octopetala* specimens is crenate-dentate and branched hairs are present on the lower midvein. Clearly, the taxonomical criteria used in the two approaches are up to this point almost identical.

But, according to Hultén and Elkington, the crosses between the species which they recognize, particularly *D. integrifolia* and *D. octopetala*, are common and produce hybrids with characteristics which are intermediate to those of the parental species. Certain hybrids, by way of an allopatric or sympatric evolution mechanism, appear to be acquiring an increasingly independent status and can therefore reproduce while maintaining their phenotype. These morphogenotypes are treated as subspecies by Hultén (1959), who also distinguishes varieties in the case of the more plastic phenotypes. These phenotypes to which Hultēn grants the taxonomical status of variety correspond to the expression of the environmental influence combined with a slight genetic differentiation: they are ecotypes.

Thus, most of the differentiations made by Porsild (1947) at the species level are placed at the subspecies or the variety level, if they are recognized at all. *D. crenulata* Juz. is considered by Hultēn (1959) to be a hybrid between *D. integrifolia* ssp. *sylvatica* and *D. octopetala* ssp. *alaskensis*. *D. crenulata* is, according to Hultēn, only a viscid variety of *D. octopetala* L. *D. alaskensis* Porsild becomes *D. octopetala* ssp. *alaskensis* (Pors.) Hult.

The taxonomical treatment used for the genus in the North American floras varies between the two extremes described above. Anderson's flora, revised by Welsh (1974), uses a very cautious conservative approach, recognizing only *D. Drummondii*, *D. integrifolia* and *D. octopetala* as species and subdividing the last two only crudely with subgroups the characteristics of which belong to several distinct types in both extreme classification schemes (Porsild 1947, Hultēn 1959).

Hultēn (1968) adopts a rather conservative treatment based on his 1959 study. Omitted are certain races which had been given subspecies or variety status in 1959 and which are known to be present in the region covered by the flora. At the other extreme, the Norhwest Territories flora of Porsild and Cody (1979) uses the classification scheme devised by Porsild in 1947. Wiggins and Thomas (1962) adopted Porsild's approach to classify the types present in the septentrional portion of Alaska covered by their flora. Finally, Taylor (1970) also adopted Porsild's treatment for those specimens which correspond to *D. Hookeriana* Juz. but used Hulten's nomenclature for the lowland specimens with entire leaf margin (*D. integrifolia* ssp. *sylvatica*). This rapid survey of the taxonomic treatment given to the genus illustrates the variety of approaches which have been taken so far. Evidently, the choice of classification is bound to influence the perception one has of the variety of phenotypes in a given region.

McGraw and Antonovics (1983) studied the phenotypic variations of *D. octopetala* L. Two extreme forms classified as subspecies by Hultén (1959) as well as intermediate forms to these were found at the study site. Following field and laboratory experiments, they concluded that the two extreme forms *(D. octopetala* ssp. *octopetala* and *D. octopetala* ssp. *alaskensis)* are ecotypes. The pubescence characters used to distinguish the two were not affected by reciprocal transplantation in the field. This appears to confirm some of Hultén's opinions on the nature of the variation. According to McGraw and Antonovics, the greater phenotypic plasticity of the *alaskensis* ecotype suggests that it probably originated from the same evolutionary branch which first produced the *octopetala* ecotype. Biogeographical and macrofossil evidence was also cited to support this hypothesis.

As we have seen, there is much controversy involved in the taxonomic classification and, more importantly for this study, in the distinction of the various types of the genus. This problem is fundamental when trying to circumscribe the variability of a genus for a given region. Knapp (1984) has examined the importance of species differentiation and hybridization in vegetation analysis and concludes that the taxonomic treatment of genera of any complexity in a given flora is more often than not seriously deficient because much of the evidence upon which a given taxonomical distinction was made is absent. This deficiency of floras is inherent to the need for a "very condensed and specialized format" (Knapp 1984).

As stated by Knapp (1984), hybrids and introgresssions can involve cognitive aspects of as much importance as species, subspecies and varieties for the taxonomic structure or the analysis of distribution. "Several ecotypes, namely in the form of discontinuous races, can be identical to morphologically differentiated and already described taxa (closely related species, subspecies, varieties, etc.). Most of the ecotypes, however, have not been circumscribed and named with the traditional taxonomical methods..." (Knapp 1984). The three most recent and important works on the genus are now at least twenty years old (Porsild 1947, Hultén 1959, Elkington 1965), with the obvious methodological implications that we know, especially in the case of quantitative analysis.

It therefore seems imperative to develop a typology adapted to the reality of the problem at hand, namely the determination of the pattern of variation of the genus at the regional and local scales. This typology will be based on morphological characters chosen for their significant discriminating qualities. Here the review of taxonomical treatments of the genus becomes particularly useful since it suggests those characteristics most likely to provide useful morphological distinctions. Such is the case of several leaf characters repeatedly mentioned in the literature: degree of crenation, relative size, various gland densities on the upper and lower surfaces, shape of the leaf base. Characteristics related to other parts of the plant will have to be examined closely as well before any final selection of characters is made.

3.2 General Botanical Description and Floral Biology

Albeit scantily so, the morphology and reproductive strategy of the genus have been studied. Porsild and Cody (1979) give a typical description for members of the genus:

> "Low, mat-forming undershrubs, with freely rooting branches. Leaves leathery, tardily deciduous, petioled, simple, crenate or entire, dark green and mostly glabrous above, white-tomentose beneath. Stipules linear-lanceolate, rising from the leaf-axils, tomentose and usually with gland-tipped hairs. Flowers scapose, normally solitary. Hypanthium saucer-shaped, flattened or convex. Sepals and petals eight to ten, the petals white or pale yellow: stamens and pistils numerous, the style terminal, persisting, much elongated and plumose in fruit."

We will look principally at the alpine members of the genus. Jessen (1921) studied the two main alpine types, *octopetala* L. and *integrifolia* M. Vahl, and also reviewed previous work done on the two species. Elkington (1965,1971) worked extensively on their biogeography in Greenland and Great-Britain, and included a number of observations on their morphology and reproduction.

As mentioned previously, their morphological differences are few (Jessen 1921). *Dryas* individuals can probably all potentially live for a fairly long time. The maximum recorded age is 108 years old for a specimen of *D. octopetala.* Ages of over fifty years have been commonly recorded (Elkington 1971, Jessen 1921). They are woody chamaephytes which can grow to a height of 5 to 10 cm, depending on the species, and form individual patches which commonly average 0.5 to 1.5 m in diameter. The local populations are generally composed of a considerable number of individuals. Mature leaves may be retained over winter but usually become senescent in the fall and are gradually lost. Immature leaves are normally retained and expand in the following spring, allowing for a quick pick-up of the growth rate (Elkington 1971).

The main period of flowering is reported to be June-July in montane and alpine sites but smaller numbers of flowers can be produced throughout the summer (Elkington 1965,1971). A differential phenology has been reported for the *octopetala* and *alaskensis* ecotypes by McGraw and Antonovics (1983), but there is much overlap between the flowering times. Despite the overlap, the authors report that pollen flow between the two ecotypes was greatly reduced because of the separation. More than 99% of the pollen flow was between plants of the same ecotype (McGraw and Antonovics 1983). In fact, the lack of pollen exchange between the two ecotypes in nature may well be due primarily to the spatial segregation of the populations and the relative shortness of individual pollinator flights. The flowers of both *D. octopetala s.l.* and *D. integrifolia s.l.* are mainly hermaphrodite and generally homogamous (Jessen 1921, Elkington 1971). Slight proterogyny and proterandry have also been reported (Jessen 1921).

The pollination is reportedly done by insects. Members of the Diptera appear to be the more frequent visitors (Hocking and Sharplin 1965, Elkington 1971). Individual pollinator flights have been found generally not to exceed 3m by McGraw and Antonovics (1983). Elkington (1971) reported evidence for a self-incompatibility system in *D. octopetala*, and defines reproduction as amphimictic. Experimentally, McGraw and Antonovics showed that there was no apomixis, no auto-fertility or self-fertility for the ecotypes *octopetala* and *alaskensis*, and thus concluded that there was apparently no breeding system barrier to gene flow between the two. In fact, Porsild (1959) stated that the ease with which two species as well separated as *D. Drummondii* and *D. octopetala*, each belonging to different section, can artificially be crossed to produce *D. Sundermanii* is an indication of the possible absence of genetic barriers within the genus.

Effective reproduction is usually by seed, although there is some vegetative reproduction by adventitious rooting of old stems (Jessen 192, Elkington 1971). The seeds are comose (plumed) diaspores obtained by persistence of the style on the achene and deployment of long lateral hairs on the style and pericarp. They are therefore well suited for anemochory (Pijl 1972, Elkington 1971, Jessen 1921). Wind patterns, past and present, may therefore have been and be of crucial importance in the past and present colonization and invasion events.

3.3 Ecology

Few studies have dealt specifically with the ecology of the genus or certain of its members. Most ecological references and generalizations have been made in a taxonomical or botanical context (Hultén 1959 and 1968; Porsild 1947, 1957, 1959, 1966 and 1974). Some researchers have contributed specifically to the ecology of the genus (Elkington 1965 and 1971, McGraw and Antonovics 1983, McGraw 1985). However, with the exception of the 1965 study by Elkington, the research tends to focus on one particular species: *D.*

octopetala s.l. Consequently, most information regarding the ecology of other species has to be gleaned from the taxonomical, botanical and synecological studies. Further, the information obtained from the latter category has to be used with circumspection because of the all too often unreliable quality of the identification.

Dryas has a circumpolar and boreal distribution. In temperate regions, it is also found in alpine and subalpine areas (Jessen 1921, Porsild 1947). The genus is generally regarded as calcicolous (Porsild 1957 and 1975, Elkington 1971) or even calciphilous (Porsild 1979). Elkington (1971) qualifies his statement by adding that a comparatively high base status is maintained in all soils where *D. octopetala* L. is found, whatever the geological origins. In the twelve soils which he tested, combined exchangeable calcium and magnesium did not drop below 60% of the total exchange capacity of the major cations determined, with one exception at 51%. The same author (1965) states that, in Greenland, *Dryas* grows under a variety of soil conditions in the field study area. He found that soil pH ranged from 5.5 to 8.1 and reports a study by Lunde in 1962 with a range of 4.5 to 8.3. Other authors have reported the association of lime-rich rocks and *Dryas.* Elkington (1971) mentions that: "In North America Bamberg and Major (1968) state that in Montana *D. octopetala* is an indicator of calcareous substrata, with soil pH ranging from 6.2 to 7.8, but cite work by Murdock (1951) and Willard (1963) which indicates that in the southern Rocky Mountains it may be present on acidic soils". For Porsild and Cody (1979): "All members of the genus, but especially *D. Drummondii,* are distinctly calciphilous. Therefore, the presence of *Dryas* on non-calcareous bed rock or on soils derived from such rocks, indicates the presence of local calcicolous mineral veins or of glacier or water transported calcareous soil particles".

D. octopetala L. and *D. integrifolia* M. Vahl are pioneer species of open habitats (Elkington 1971, Porsild 1957). The genus is present in a considerable range of communities

(Elkington 1965). This may be related to its ability to fix nitrogen in root nodules, a capacity which has been confirmed for *D. integrifolia, D. octopetala* and *D.Drummondii* (Elkington 1971)

Using the nomenclature devised by Porsild (1947), we will now examine the ecological characteristics which have been attributed to the various species by Porsild and Cody (1979) and Hultén (1968). *D. octopetala* and *D. integrifolia* have both been reported as ubiquitous species. The former is generally attributed an amphi-Beringian distribution, the latter, a North-American one. Both are found mainly in herbaceous tundra but *D. octopetala* may be able to colonize at greater altitude than *integrifolia* (Hultén 1968). *D. crenulata* and *D. punctata* are reported by Porsild and Cody (1979) to have life habits similar to *octopetala*. *D. Hookeriana* and *D. alaskensis* are reportedly both common in or near snowbeds in alpine environments. Both also have amphi-Beringian distributions, albeit more sporadic ones. *D. sylvatica* is a subalpine and lowland forest species endemic to the northwestern portion of North-America. Lastly, *D. Drummondii* is a chiefly lowland species in subarctic areas but is found in the alpine zone in more temperate North-American latitudes.

Relatively few studies have been undertaken in the Kluane and Ruby Ranges concerning the spatial and ecological distribution of alpine vegetation. Botanical collections have been made (Porsild 1966, Hultén 1968), but no regional study of alpine vegetation has been attempted. Porsild (1966) reports the presence of *D. alaskensis* and *D.octopetala* in the northwestern and central sectors of the Ruby Range, and that of *D. crenulata* and *D. Hookeriana* in the southeastern portion of the Kluane Ranges.

In the Ruby Range, Price (1971) has studied the vegetation of a localized area and looked at the influence of exposure, depth of active layer and microtopography on the vegetation. A 1969 paper by Price on aspects of solifluction also mentions the genus. In both cases, only *D. octopetala L.* is reported.

In the Kluane Ranges, the vegetation ecology of Sheep Mountain was studied by Hoefs et al. (1975) who reported finding *D. integrifolia* M. Vahl ssp. *integrifolia* exclusively in the alpine zone. In 1981, Grier and Ballard conducted an ecological study in the area immediately to the south where they identified *D. integrifolia* Vahl. In the Grizzly Creek valley, approximately 30km west-northwest of Sheep Mountain, Lambert (1982) and Leverton (1981) found *D. octopetala* L. As part of a palynological study, Birks (1977, 1980) studied the present vegetation of the eastern moraines of the Klutlan Glacier and reported *D. integrifolia* ssp. *integrifolia* Hult. and *D. octopetala* ssp. *alaskensis* as alpine species.

This information will be reexamined later, in the light of the results of the present study. However scant, it may permit certain comparisons and parallels which could prove very useful in ascertaining the consequences of the results in the determination and interpretation of the distribution of the genus in the study area.

Chapter IV

CONCEPTUAL FRAMEWORK

The study of plant distribution patterns is necessarily multidisciplinary. As the words imply, this type of study is related to botany by the object, the plant, and to geography by the subject, spatial distribution. In fact, biogeography, which evolved in part from the work of early eighteenth century naturalists such as Humboldt (Stott 1984), attempts to circumscribe those research questions which deal with this duality. In spite of a growing interest in the questions of distribution of biological organisms, biogeography remains a discipline torn by proponents of the biological and geographical traditions:

> "Biogeography is currently developing apace. However, a classical origin does not necessarily ensure a modern identity in the continuing struggle between the 'hard' and 'soft' sciences. The different forms and rates of development in the geographical and biological sciences have given biogeography a kind of double identity which has served only to confuse and delay its establishment as a separate science"(Taylor 1984).

Some of the definitions which have been given for biogeography can only perpetuate the problem: "the biological study of the geographical distribution of plants and animals" (Morris 1976). Pianka (1978) defines it as the study of "spatial distributions of plants and animals over large geographic areas..." to distinguish biogeography from ecology, one of the major goals of which is to understand the influence of various factors on the microgeographic distribution of living organisms (Pianka 1978).

In fact, an examination of the history of biogeography and ecology demonstrates the important overlap between the two, an unavoidable consequence of their basic respective definitions (Stott 1984). Ecology, defined as "the study of the relations between organisms and the totality of the physical and biological factors affecting them or influenced by them" (Pianka 1978), was quickly integrated to the biological sciences with which it undoubtedly has the most affinity in many respects. This may well explain the relatively recent appearance of yet another related discipline or research field, landscape ecology —many proponents of which are geographers—, which seeks to formally reintegrate the concept of space in studies of an ecological nature (Phipps 1981a, Naveh and Lieberman 1984, Forman and Godron 1986). Risser, Karr and Forman (1984) see landscape ecology "not as a distinct discipline or simply a branch of ecology", but as the "synthetic intersection of many related disciplines that focus on the spatial and temporal pattern of the landscape". The work herein uses many concepts derived from landscape ecology since the latter "considers the development and maintenance of spatial heterogeneity" as well as "the spatial and temporal interactions and exchanges across heterogeneous landscapes" (Risser, Karr and Forman 1984). Another discipline which attempts to delineate the study of the distribution of living organisms is areography, a term coined by Rapoport (1982) who equates it to chorology and defines it as the "study of the geographical ranges of taxa". Again, this research has much to gain from the borrowing of some of its concepts related to dispersal as a diffusion process, barriers to dispersal and their porosity, and the loss of biotic resemblance with distance.

This thesis examines the geographical distribution of a genus of plants and attempts to relate the patterns to environmental and biological factors. Its questions are therefore classically biogeographical, although some aspects of the research undeniably have strong ecological connotations. But this is the study of a particular problem of plant distribution from a geographical perspective, by placing as little emphasis on the biological aspects of the question as possible, keeping in mind the interdisciplinary nature of such work.

It is the interdisciplinary nature of any biogeographical question which makes allegiance to a single well defined discipline such as botany or ecology impossible, not that such academic singularity is particularly or necessarily desirable. This thesis borrows concepts and ideas from a range of specialized fields which have important implications in the study of phytogeography. The quantitative methods of discrimination developed in numerical taxonomy and ecology, and the conceptual approaches of taxonomy and biosystematics have proven greatly valuable in the development of a sound procedure for the measurement and the analysis of the geographic variation (Sneath and Sokal 1973, Snaydon 1984, Sokal 1983, McNeill 1984, Legendre and Legendre 1983). In fact, the study of geographic variation is emerging as a distinct field of specialization (Endler 1983 and 1977, Sokal 1983, Thorpe 1983). Endler (1983) has developed a conceptual framework for the testing of causal hypotheses in the study of geographic variation. Phenotypic variation patterns involve three basic components: historical factors, current ecology and random variation. Any explanation attempt has to contend with these components.

Although the phenotype is not necessarily an accurate expression of the genotype because of phenotypic plasticity and random variation, it is generally accepted as a fair indicator of genetic distinctiveness, in the absence of direct genetic evidence (Thorpe 1983, Snaydon 1984). For it is the genotype which ultimately determines the characteristics of a given living organism. Because of this, we must also examine certain aspects of genetics pertaining to populations or demes (Pielou 1979, Mitchell-Olds and Ruthledge 1986) and their differentiation when in close proximity (Jain and Bradshaw 1966, McNeilly and Antonovics 1968), gene flow or migration (Pielou 1979, Bull et al. 1987) and speciation (White 1978, Pielou 1979).

Chapter V

DEFINITION OF SCOPE

The primary objective of this research is to determine the regional distribution pattern for each of the major types of *Dryas* identified in the Ruby and Kluane Ranges of the southwestern Yukon Territory. This objective implies the necessity to develop an appropriate regional typology since the existing identification schemes may have serious limitations which could in effect create artificial or misleading results. Once the typological analysis complete, a proper identification procedure will have to be defined. Only then can the distribution patterns identified be related to environmental factors. Because of the duality of scales, these factors can be regional (climate, geology) or local (microclimate, edaphic factors). As mentioned above, there is also a chronology of the factors to be considered (contemporary or historical), although only contemporary factors are likely to be measured with any accuracy. One special factor which has to be examined is space as structuring agent of the genus through the spatial processes of diffusion and contagion.

We will therefore examine the following questions:

1. Within the genus, what types can be identified for the region and what are their respective morphological characteristics?
2. What are the relationships between the various types identified?
3. What is the regional distribution pattern of each type?
4. Are there significant local patterns in the distribution of the phenotypes? If so, at what scale of the landscape do they occur?
5. What regional factors contribute to the explanation of the regional distributions?
6. What local factors contribute to the explanation of the local distributions?

7. What is the role of space in the distribution pattern?

8. To what extent do the patterns, regional and local, appear to be explained by the present environmental conditions? In other words, to what extent, if any, has the pattern become independent of environmental conditions and what may have contributed to this?

Chapter VI

METHODOLOGY

The methodology of this biogeographical study involves three major procedures: specimen and data collection in the field, morphological analysis of the specimens, and multivariate analysis of the morphological and ecological data. In the field, the primary goal was the systematic gathering of individual *Dryas* specimens and pertinent ecological information at each site. Therefore, in this instance, the methodological questions had to do with the design of an efficient sampling scheme and the choice of field variables to be recorded. The second methodological step, namely the morphological analysis of the specimens, also required a sampling method —albeit a much simpler one— but, more importantly, the choice of those morphological characteristics to be considered in the study and their measurement. Finally, the analytical procedure proved to be more complex in design than either previous procedure. It comprises three major steps: a typology of the specimens based on the subsample used in the morphological analysis and recorded morphological variables, an identification of the specimens not included in the subsample of the morphological analysis, and lastly, a multivariate analysis of the geographical ecology of the various types of *Dryas* identified in the study area.

6.1 Field Methods: Data Collection and Specimen Gathering

The dual nature of the study —regional and local— necessitated a sampling design which would take this duality into account. Several stratified sampling methods would have been appropriate (Cochran 1977, Frontier 1983) but limitations of a practical nature further reduced the possibilities. Because of the nature of the distribution of the genus Dryas and the specific interest in alpine species, sampling was to be conducted above 4500', with the consequence that, regionally, the sampling method would be applied on a number of relatively well segregated alpine tundra 'islands', each with its potentially unique mixture of *Dryas* types. Each alpine island possesses demes (Pielou 1979) --distinct populations of *Dryas* between which gene flow does not take place on a regular basis-- the number of which is potentially related to various ecological parameters such as mesotopography, microtopography, wind patterns, type of pollinators, and various edaphic parameters, as well as to intrinsic properties of the individual populations.

With limited accessibility and meager financial resources, what little time could be spent sampling in the field had to be used as efficiently as possible. These constraints eliminated any random sampling system outright. Any type of random sampling would have been too costly in time, effort and financial resources since it would have dispersed the sampling sites unnecessarily and unreasonably given the difficult nature of the terrain. Furthermore, available information concerning surficial geology which may hypothetically be assumed to influence plant distribution made possible the subdivision of the region under study into geological sub-units of different areas. To maximize information gain, systematic sampling throughout the region, stratified to account for the regional physiography and geology was chosen as the most appropriate and efficient method. Regular spacing of information is most efficient in recovering the true spatial pattern as long as the pattern does not involve repetitions at a frequency equal to that of the sampling (Frontier 1983, Cochran 1977), which is not the case at the regional scale and extremely unlikely at the local scale.

Primary stratification was therefore by range: both the Kluane and Ruby Ranges were sampled systematically. The 1985 season was spent sampling in the Ruby Range while the Kluane Ranges were the focus of the 1986 field season. The difficulty and cost of access to various sectors of the Ruby Range resulted in a smaller subsample size for that stratum, but this problem was offset by the relatively simple specimen distribution throughout most of the range. The Kluane Ranges generally offered easier access and hence more economical sampling. Secondary stratification by geological units, while straightforward for the Ruby Range since the systematic sampling of the range automatically resulted in a stratification by geological unit, was obtained at the alpine island or local level in the Kluane Ranges. This is because the geological units which generally cover several alpine islands each in the Ruby Range are usually intermixed in various combinations within each major alpine island of the Kluane Ranges.

At the local scale, within the sectors designated for sampling, systematic transects were used as the subsampling method. Again, because of the nature of the terrain, this is a particularly well adapted and realistic method. In each sampling sector, depending on topography and area, a transect was devised with the objective of sampling at all altitudinal levels while covering the sampling sector as thoroughly as possible for the maximization of information gain and, in the case of the Kluane Ranges, taking into account the geological units to be traversed. The discrepancy in stratification is thus compensated for by the systematic subsampling of the alpine islands in the Kluane and Ruby Ranges. The result was therefore the same for both ranges: a regionally systematic sample with geological stratification, subsampled systematically at the local level.

At each individual sampling site, a circular area with a 1m radius was sampled systematically in a clockwise fashion so as to result in the taking of 8 individual specimens, some of which could be discarded later should an examination with a 25X hand microscope indicate unnecessary repetition of a given set of characters in many of the specimens. While a minimum of eight specimens were initially taken at each site, more specimens were taken when it was felt that the sample did not include all the visibly different types. The sampling method was thus devised as a way of ensuring a minimum number of specimens in those areas where there was little or very subtle variation. At each site, the following variables were recorded: altitude a.m.s.l., relative altitude, slope, orientation of the slope and soil depth. Six classes of relative altitude were used to cover all situations encountered: summit, upper slope, intermediate, lower slope, basin, ridge crest. Soil depth was defined as the depth to the C-horizon or that of the active layer. A subterranean rock sample and a soil sample in the rooting layer were also taken.

6.2 *Morphological Analysis*

A first summary examination of specimens taken at random was made to study the adequacy of the morphological variables originally chosen. After several trials and adjustments, the variables appeared to adequately reflect the characteristics which they were devised to represent and systematic recording of measurements could begin.

The morphological analysis was done on a subsample of the specimens retained after the discarding of unnecessary replicates. Two sites located at the extremes of altitude were taken for each major transect for a total of 83 individual plant specimens. Additionally, at least two mature leaves were sampled per plant specimen. In cases involving much variation, as many as five leaves were sampled for a total of 175 observations. This subsampling by taking for each transect the specimens from the two sites which represent the altitudinal limits is perceived as the method providing the best chances of sampling all the types of *Dryas* to be found given the constraint that only two sites were to be used by transect and the knowledge concerning a certain altitudinal stratification of the types of *Dryas* (Hulten 1968, Porsild and Cody 1979). The limitation of subsampling to the specimens of two sites per transect was made necessary by the number of quantitative variables to be measured --14 in all-- which rendered the analysis procedure extremely time consuming. A Wild Heerbruug binocular microscope with 12X to 100X magnification coupled to a

Volpi Intralux 6000 illuminator was used for all the measurements, which were recorded to the nearest tenth of a millimeter. Linear measurements were made at a 9X magnification while density counts were done at a magnification of 50X, with some verifications at up to 100X.

The characteristics were chosen in an attempt to give as complete a representation of the morphological variability within the genus as possible. The choice was based on a combination of the information available from past studies, field observation and microscopic examination. The variables were designed to reflect the morphological characteristics quantitatively and with reasonable accuracy. The result was a set of 14 measured variables per observation or leaf specimen. Some of the variables are straightforward length measurements, others are measures of the density of a particular feature. They are:

1- Length of the leaf (LENGTHMM), measured from tip to petiole attachment;

2- Maximum width of the leaf (MAXWIDMM), measured perpendicular to the midvein for a completely flattened leaf, a rule which required that estimates be made in the case of strongly revolute margins.

3- Width of leaf base (BASWIDMM), one of two variables designed to reflect the shape of the leaf base quantitatively. This variable is the width of the leaf at the point of attachment of the petiole, measured perpendicularly to the midvein. This resulted in a very small value corresponding to the width of the petiole in the case of elliptic leaves or any leaf with an acute or cuneate leaf base. Ovate leaves or other leaf types with a rounded leaf base had more substantial values for the variable but, on average, the larger values were measured for leaves with cordate or truncate bases. A special case was that of the oblique base which resulted in rather intermediate values.

4- Length of petiole-leaf overlap (PETLENMM), measured from the point of attachment of the petiole to the intersection with the perpendicular to the leaf base. This definition resulted in null values for cuneate, acute or absolutely truncate bases while cordate and oblique had the larger values. The combination of this variable with the previous one allows a reasonably good quantitative discrimination of the various base shapes found within the genus. It should be noted that there was most often a certain gradation between shapes, a fact which cannot be reflected as clearly with qualitative variables.

5- Number of indentations around the leaf (NUMINDEN), a simple count. It was chosen not to use only one side of the leaf since the number of indentations can vary quite considerably from side to side at times.

6- Crenation depth (CREDEPTH), measured perpendicular to the midvein and on the deepest indentation.

7- Density of sessile glands on the lower midvein (LOWSESSI), counted over a predetermined surface of the midvein, a thin rectangular band, so as to avoid the problem of extreme midvein widths. The count was always begun at the point of attachment of the petiole. These rules also hold for the other two density variables for the lower midvein.

8- Density of stalked glands on the lower midvein (LOWSTALK), counted according to the same rules as LOWSESSI.

9- Density of branched hairs on the lower midvein (LOWBRANC).

10- Density of sessile glands on the upper leaf surface (UPSESS), obtained by counting the number of these glands within a predetermined rectangular surface which could be accommodated by all leaves.

11- Density of stalked glands on the upper leaf surface (UPSTALK), measured in the same fashion as the previous variable.

12- Density of hairs of the upper leaf surface (UPHAIRD), also measured like UPSESS.

13- Density of stalked glands on the peduncle (PEDUNCLE), counted over a predetermined length of the stalk.

14- Density of stalked glands on a sepal (SEPALDEN), counted over a predetermined rectangular surface chosen to fit all sepal sizes.

In addition, 4 relative variables were generated by combining some of the linear variables into ratios. The relative indentation variable (RELINDEN) is the ratio of the number of indentations (NUMINDEN) over leaf length (LENGTHMM). The ratio of leaf length over maximum width (MAXWIDMM) gave the relative size (RELASIZE). RELABASE is the ratio of BASWIDMM over MAXWIDMM. Lastly, the relative depth of crenation (RELACREN) is the ratio of CREDEPTH over MAXWIDMM. From the data of this morphological analysis, a matrix of 175 observations by 18 variables was created which was then used in the next analytical step, the typology of the genus. Finally, a univariate analysis of each variable was performed for the 175 observation matrix.

6.3 Multivariate Analysis

6.3.1 Typology

The data obtained from the morphological analysis of the systematic subsample were used to create a typology of the genus for the study area. This typology involves two steps and two multivariate methods. The first step is the multivariate analysis of the morphological data by ordination; the second step is the cluster analysis of the data as structured by the ordination. The multivariate methods used to accomplish these steps are both SAS procedures. The ordination method chosen was principal factor analysis while clustering was done using the k-means method for non-hierarchical clustering analysis. As we will see, these two steps had to be repeated once to provide a better typology of certain hybrid types.

6.3.1.1 Principal Factor Analysis

Principal factor analysis is the simplest and computationally most efficient method of common factor analysis (SAS Institute 1985). It is the application of the method of principal components to the reduced correlation matrix, in which communalities occupy the principal diagonal (Harman 1976). Gauch (1982) states: "Instead of trying to account for as much of the total variance as possible, only correlations between variables are of interest as reflecting putative underlying causes or factors... Computationally, factor analysis is an eigenanalysis problem". Since the goal of factor analysis is to account for the covariance between descriptors and since the common factor model assumes that the measured variables are combinations of hypothetical underlying factors (Harman 1976, SAS Institute 1985), the result of a factor analysis is the representation of "the covariance structure of the descriptors in terms of hypothetical model" (Legendre and Legendre 1983).

In the common factor model of analysis, two types of underlying factors are assumed: common factors, which contribute to at least two of the measured variables, and unique factors, which "play the role of residuals and are defined to be uncorrelated both with each other and with the common factors" (SAS Institute 1985). Only the variance related to common factors is relevant in principal factor analysis. The part of the variance of each variable "which is accounted for by the common factors" is called the communality (Legendre and Legendre 1983). The result of principal factor analysis is the determination of a number of orthogonal --hence uncorrelated-- factors which "account for the covariation among a much larger number of observed descriptors" (Legendre and Legendre 1983). The initial extracted factors are often rotated by the application of a nonsingular linear transformation. This rotation usually results in a simpler structure in which the factors are still uncorrelated if an orthogonal transformation is used. Rotation does in no way change the proportion of the total covariation which is accounted for by the principal factors (SAS Institute 1985, Legendre and Legendre 1983).

Principal factor analysis is well suited for the determination of major phenotypes from morphological data. Clifford and Stephenson (1975) recommend it over principal components analysis when the data include a large proportion of attributes which are only weakly intercorrelated. This is the case here since the use of morphological data necessarily implies random variation of characters and phenotypic plasticity which act as noise superimposed on that portion of the phenotype which is a truer reflection of the genotype.

The first principal factor analysis was performed on the 175 observation matrix described above for combinations of the variables which either included or excluded the relative variables. The combination with the best overall measure of sampling adequacy was retained and improved by the removal of those variables with unacceptable individual values for Kaiser's measure of sampling adequacy (SAS Institute 1985). The factor solution retained was then tested using another common factor method to determine the best number of factors. Maximum likelihood analysis is an iterative method which can be used to check the principal factor solution (SAS Institute 1985). The quartimax rotation method, an orthogonal transformation method which minimizes the sum of squares for the products of the loadings of each variable for the factors retained (Legendre and Legendre 1983) was used to simplify the factor pattern. Clusters were then created on the basis of the simplified factors as described in the next section.

A second factor analysis had to be performed on some of the groups obtained after clustering to reorganize the clusters into more homogeneous groups. This analysis was performed on extracted data in the same manner as the first one but did not involve orthogonal rotation. The factors obtained were used in a clustering of the extracted observations.

6.3.1.2 Cluster Analysis

A disjoint clustering method of the SAS statistical package called FASTCLUS was used to create groups on the basis of the two principal factor analysis solutions. This method "performs a variation of what is called the k-means method for non-hierarchical cluster analysis" (Romesburg 1984). It combines an effective method for determining initial clusters with a standard iterative algorithm which seeks to minimize the sum of the squared distances from the cluster means (SAS Institute 1985). The k seeds are initially selected so as to maximize the Euclidean distance between them. The clusters are "formed by assigning each observation to the nearest seed" (SAS Institute 1985). Several options exist which form temporary clusters the means of which change each time a new observation is added on. The clusters can be stabilized by iterating the chosen options (SAS Institute 1985, Romesburg 1984).

The FASTCLUS method is claimed to be well suited for the cluster analysis of data sets containing over 100 observations, and to be good at finding initial cluster seeds. The SAS statistical manual (1985) also indicates that stable clusters are usually found after only a few iterations.

The clustering procedure was applied to the principal factors retained for each of the factor analyses. The probable minimum and maximum number of clusters were easily determined in each case since both factor solutions involve two factors. The cluster analysis was then performed for the various cluster numbers. The clustering which resulted in the most realistic and homogeneous groups was retained in each case and improved by modification of the options. Because the method was used with principal factors, no standardization of variables was necessary. The k-means method tends to be biased toward the creation of clusters of the same size (SAS Institute 1985) but this was not a problem since the structure of the dispersion diagram indicated the existence of several clumps of roughly the same importance. The clusters obtained were tested with a canonical discriminant analysis method to see how the discriminant function interpreted the clusters (Legendre and Legendre 1983, SAS Institute 1985). Lastly, univariate analyses of each of the significant variables were performed for each cluster and for both clustering steps to determine the exact range of values in each case.

6.3.2 Identification

As was the case for the principal factor analysis and the cluster analysis procedures, the identification procedure had to be repeated to determine more accurately the phenotypic composition at each site. Each identification first involved the selection of pertinent variables. This selection was based primarily on the principal factor solutions, but also on an efficiency criterion since the variables had to be measured on the remainder of the specimen sample. In the case of the first identification step, 6 variables were chosen: RELINDEN, RELASIZE, LOWBRANC, LOWSTALK, LOWSESSI and UPSESS. Consequently, 7 variables had to be measured for each specimen. The second identification step involved only 2 variables, lowbranc and relinden, which had already been measured.

6.3.2.1 Identification Procedure

A SAS discriminant analysis procedure called DISCRIM was used on non-standardized morphological data to produce identification functions which can in turn be used to assign new observations to known clusters (SAS Institute 1985, Legendre and Legendre 1983, Pielou 1984). In fact, the method also computes the posterior probability of membership of a new observation in each of the known groups (SAS Institute 1985). Classification results are provided for the calibration data, thus allowing an appraisal of the fit of the discriminant function to the existing clusters. As mentioned above, the procedure had to be run twice. The first one served to identify most of the specimens accurately. Only those specimens which belonged to clusters for which a second principal factor analysis was necessary had to be reprocessed.

6.3.3 Ecological Analysis

The ecological analysis of the distribution patterns involves a number of variables, some of which have yet to be defined. Several of these variables are ordinal or nominal, effectively precluding the use of multivariate methods such as principal components analysis which normally require quantitative variables measured on a continuous scale. We therefore have to turn to a class of multivariate methods which can analyze categorical data.

6.3.3.1 Ecological Variables

The analysis involved three basic types of variables: regional environmental variables, local environmental variables, and distribution pattern variables. The regional environmental variables were themselves divided into three categories: geological, climatological and chorological variables. The geological variables were based on the geological maps available for the study area (Muller 1967, Kindle 1952, Wheeler 1963, Templeman-Kluit 1974). The first geological variable (GEOL) consists of 13 classes representing the various formations in the area. The second one (ROCK), has 9 classes representing generalizations of the more common rock types. LIME, the last geological variable, consists of two classes for the absence or presence of significant limestone bands in the geological formation. The rock samples from each site were used to guard against any serious discrepancies. There are three climatological variables: RAIN, for the annual rain total, SNOW, for the annual snow total, and TOTAL, for the total amount of annual precipitation. These variables are ordinal, each with five classes representing the five meteorological stations for which reliable data were available. The two chrological variables RANGE and ISLAND are categorical. The first one has two classes which stand for the Kluane and Ruby Ranges. The second has eleven categories corresponding to the eleven different alpine islands sampled. Alpine islands are, for the purpose of this variable, defined as areas surrounded by altitudes of less than 4000 feet (1250m). The local environmental variables were evaluated in the field and include the altitude (5 classes), the relative altitude(5 classes), the slope and its orientation

(5 and 9 classes respectively), and soil depth (5 classes). The distribution pattern variables are DRYAS (11 classes), representing the combinations of types found at a particular site, and RETYP, a reduced version of the DRYAS variable with 6 categories. This information was compiled for 136 sites scattered throughout the study area. The multivariate categorical analyses will be performed on the resulting matrix.

6.3.3.2 Pegase Procedure

This procedure, developed by Phipps (1981a, 1981b), is based on information theory and was first applied to the study of community types and landscape units (Phipps 1981a). Through successive divisions of the total matrix, this multivariate analytical method seeks to determine at each level which of the variables contributes most to the neguentropy. Optionally, this optimization of the divisive path can be coupled to a rule of economy whereby variables resulting in the sharpest drop in entropy will be chosen in priority. Given the low number of sites available for analysis, this divisive procedure was rapidly stopped by the rule concerning the minimum number of observations per cell. The procedure and its theoretical framework are detailed by Phipps (1981a, 1981b). The resulting divisions are usually represented by a dendrogram.

This analytical method was applied to the matrix described above to determine which variables can potentially contribute most to the explanation of the distribution pattern observed for the region. At the same time, the result may provide clues as to the role of spatial scales in the pattern.

6.3.3.3 Log-linear Model for Analyzing Categorical Data

According to Reynolds (1977): "Log-linear models are in many respects similar to well established statistical procedures such as analysis of variance and regression analysis". This technique, he contends, finally seems to put the investigation of categorical data "on a par with the study of interval-level variables". The model is discussed in detail by Bishop, Fienberg and Holland (1975). Log-linear models "do not make an a priori distinction between independent and dependent variables" (SAS Institute 1985). They emphasize model building, goodness-of-fit tests and estimation of cell frequencies for the underlying contingency table, making it easy to test for independence between variables and generalized independence (SAS Institute 1985).

A SAS procedure called CATMOD was used to test for independence and generalized independence with the log-linear model. The procedure was used to test specific questions based on the information provided by the PEGASE procedure in an attempt at model-building. It must be kept in mind that neither procedure implies any causal relationships, only covariation or association.

Chapter VII

RESULTS

7.1 *Typology*

7.1.1 First Principal Factor Analysis

The final version of principal factor analysis chosen involves eleven variables, of which four are ratios: RELINDEN, PEDUNCLE, RELASIZE, RELABASE, PETLENMM, RELACREN, LOWSESSI, LOWSTALK, LOWBRANC, UPSESS and UPSTALK. These variables were previously described in section 6.2. Several other combinations of the available variables were tried but the analysis of the combination just mentioned gives the best overall measure of sampling adequacy (Kaiser's MSA= 0.625). The partial correlations, controlling all other variables, are all smaller than the corresponding correlations, an indication of the appropriateness of the common factor model for the data (SAS Institute 1985). Two factors were retained which together account for approximately 93% of the covariation (table 1).

Table 1: Contributions of the First Three Principal Factors

```
                          PRINCIPAL FACTORS
                    1          2          3
EIGENVALUE   2.118989   1.431596   0.595848
DIFFERENCE   0.687392   0.835749   0.318996
PROPORTION     0.5576     0.3767     0.1568
CUMULATIVE     0.5576     0.9343     1.0911
```

In order to test the adequacy of the two factor solution, maximum likelihood analyses of the same eleven variables were performed for one, two and three factor solutions. The results clearly show that the two factor solution is best, as expected (table 2).

Table 2: Summary of Maximum Likelihood Analyses

	Number of Factors 1 Factor	 2 Factors	 3 Factors
Akaike's Information Criterion	315.6	195.0	Communality
Schwarz's Bayesian Criterion	192.6	148.1	greater
Tucker and Lewis's Reliability Coefficient	0.31	0.62	than 1.0

Both Akaike's information criterion and Schwarz's Bayesian criterion are at a minimum while Tucker and Lewis's reliability coefficient is maximum for the two factor solution, unanimously expressing its greater adequacy (SAS Institute 1985). In fact, the three factor solution results in an ultra-Heywood case since some of the communalities have values greater than 1.0. Such a situation implies that some unique factor has a negative variance, invalidating the solution (Harman 1976). In this case, it provides a clear indication that too many common factors are involved.

The factor pattern of the principal factor analysis before rotation are somewhat difficult to interpret since most variables contribute significantly to both retained factors (fig. 2). Before rotation, relinden and lowsessi are the major variables contributing to factor 1 while relasize and lowstalk are most significant for factor 2 (table 3). The chosen rotation method was quartimax, although both varimax and equamax gave very similar results (fig. 3).

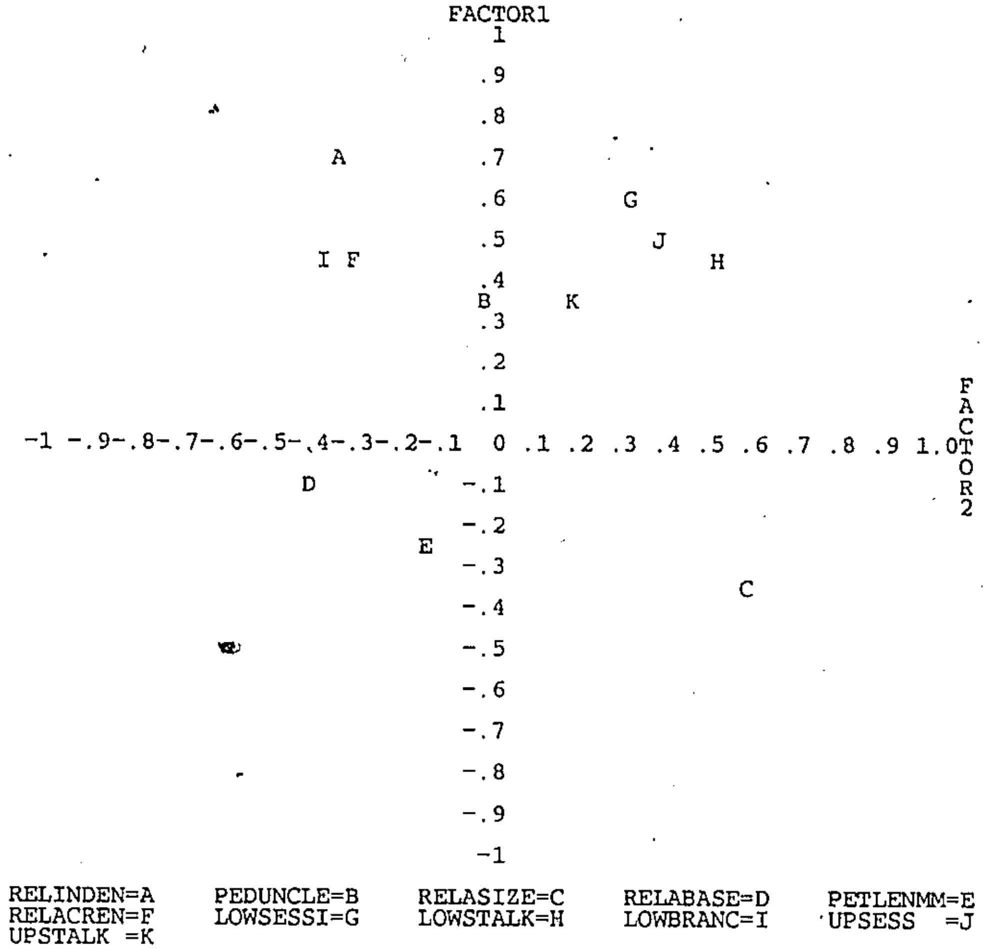


Figure 2: Plot of Factor Pattern for Factors 1 and 2 BEFORE Rotation

Table 3: Factor Pattern for Principal Factors 1 and 2 BEFORE rotation

```
                    FACTOR PATTERN

                        FACTOR1    FACTOR2

            RELINDEN    0.70584   -0.36197
            LOWSESSI    0.57508    0.31421
            UPSESS      0.49167    0.38464
            RELACREN    0.45570   -0.30337
            LOWBRANC    0.43129   -0.37098
            PEDUNCLE    0.37346   -0.00295
            UPSTALK     0.34805    0.18127
            PETLENMM   -0.24566   -0.13662
            RELASIZE   -0.33649    0.57996
            LOWSTALK    0.45639    0.52395
            RELABASE   -0.11037   -0.40227

        VARIANCE EXPLAINED BY EACH FACTOR

                  FACTOR1    FACTOR2
                  2.118989   1.431596
```

After rotation, contributing most to factor 1 are, in descending order: lowstalk, lowsessi and upsess, all gland density variables; contributing most to factor 2, in the same order, are: relinden, relasize, lowbranc and relacren. While all main variables contribute positively to factor 1 --and three to factor 2--, relasize is a negative component of factor 2: the values of this variable are inversely related to the factor (table 4).

The principal factor analysis has, on the basis of eleven of the available variables which characterize the *Dryas* specimens, defined a two-dimensional space for the regional geographic variation observed for the genus. The first dimension is defined by factor 1, a factor to which contribute positively three gland characters. The second dimension is defined by a factor which opposes the degree of crenation of the leaf and the density of branched hairs on the lower midvein to the relative size or length to width ratio of the leaf. The importance of the covariation of three gland characters as expressed by factor 1

```
                             FACTOR1
                                1

                               .9

                               .8

                             H .7
                                    G
                               .6J

                               .5

                               .4 K

                               .3      B              A

                               .2
            C                                  F                F
                               .1                               A
                                                I               C
-1 -.9-.8-.7-.6-.5-.4-.3-.2-.1  0 .1 .2 .3 .4 .5 .6 .7 .8 .9 1.0T
                                                                O
                              -.1                               R
                                                                2
                              -.2
                              E
                              -.3
                                      D
                              -.4

                              -.5

                              -.6

                              -.7

                              -.8

                              -.9

                               -1

RELINDEN=A    PEDUNCLE=B    RELASIZE=C    RELABASE=D    PETLENMM=E
RELACREN=F    LOWSESSI=G    LOWSTALK=H    LOWBRANC=I    UPSESS   =J
UPSTALK =K
```

Figure 3: Plot of Pattern for Principal Factors 1 and 2 AFTER Rotation

and that of crenation, leaf shape and branched hair density in factor 2 will be discussed in

Table 4: Rotated Factor Pattern for Principal Factors 1 and 2

```
                 ROTATED FACTOR PATTERN

                      FACTOR1    FACTOR2

          LOWSTALK    0.68937   -0.08706
          LOWSESSI    0.63828    0.14846
          UPSESS      0.62294    0.04037
          UPSTALK     0.38038    0.09649
          PEDUNCLE    0.27668    0.25086
          PETLENMM   -0.27426   -0.06163
          RELABASE   -0.35019    0.22666
          RELINDEN    0.28563    0.74004
          LOWBRANC    0.07478    0.56395
          RELACREN    0.13802    0.52976
          RELASIZE    0.13509   -0.65675

       VARIANCE EXPLAINED BY EACH FACTOR

                 FACTOR1    FACTOR2
                 1.814259   1.736326
```

the next chapter. All the variables which have been retained by the factors are based on leaf characters. Variables based on characters pertaining to other parts of the plant contribute very weakly at best. Since only two factors are involved, their dispersion diagram allows one to visualize a number of possible groups (fig. 4).

Nevertheless, a cluster analysis is necessary to distinguish clusters on the basis of the two factor solution.

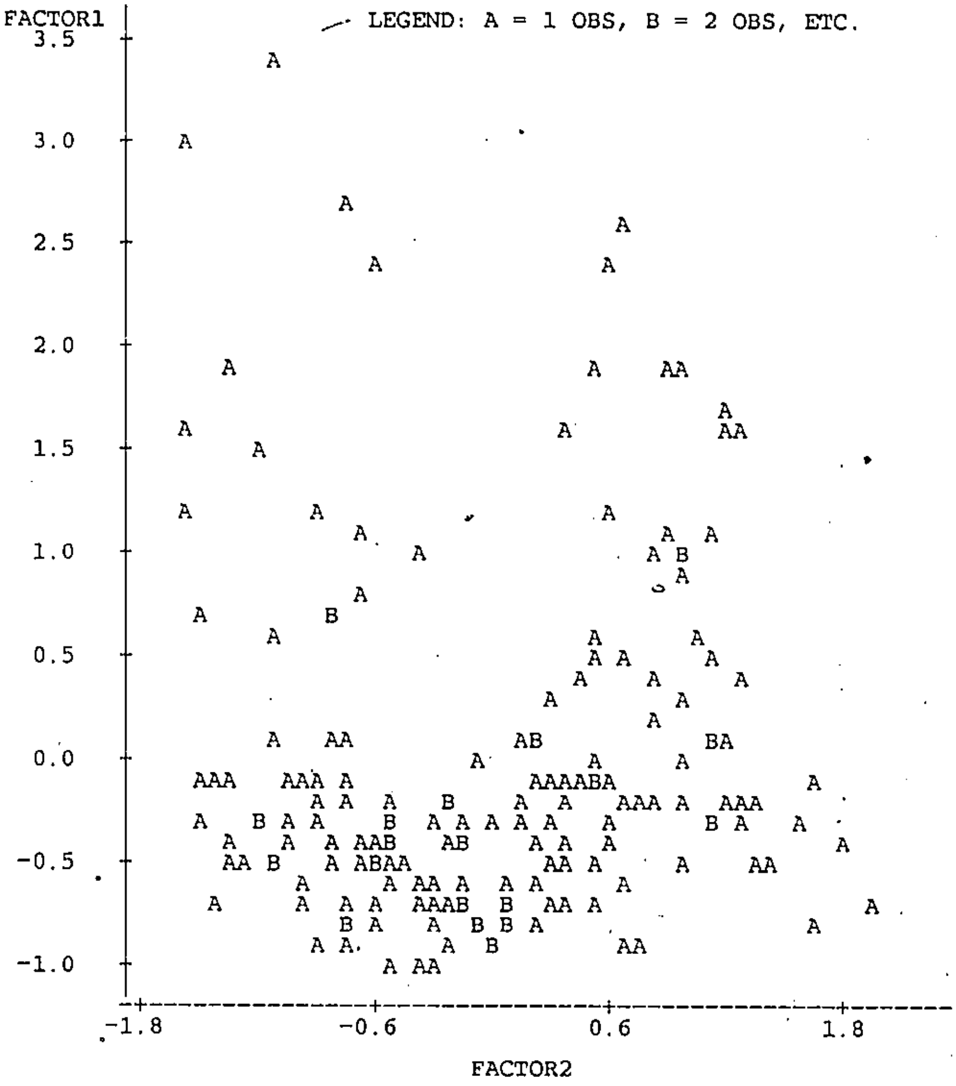


Figure 4: Dispersion Diagram for Factors 1 and 2 AFTER Rotation

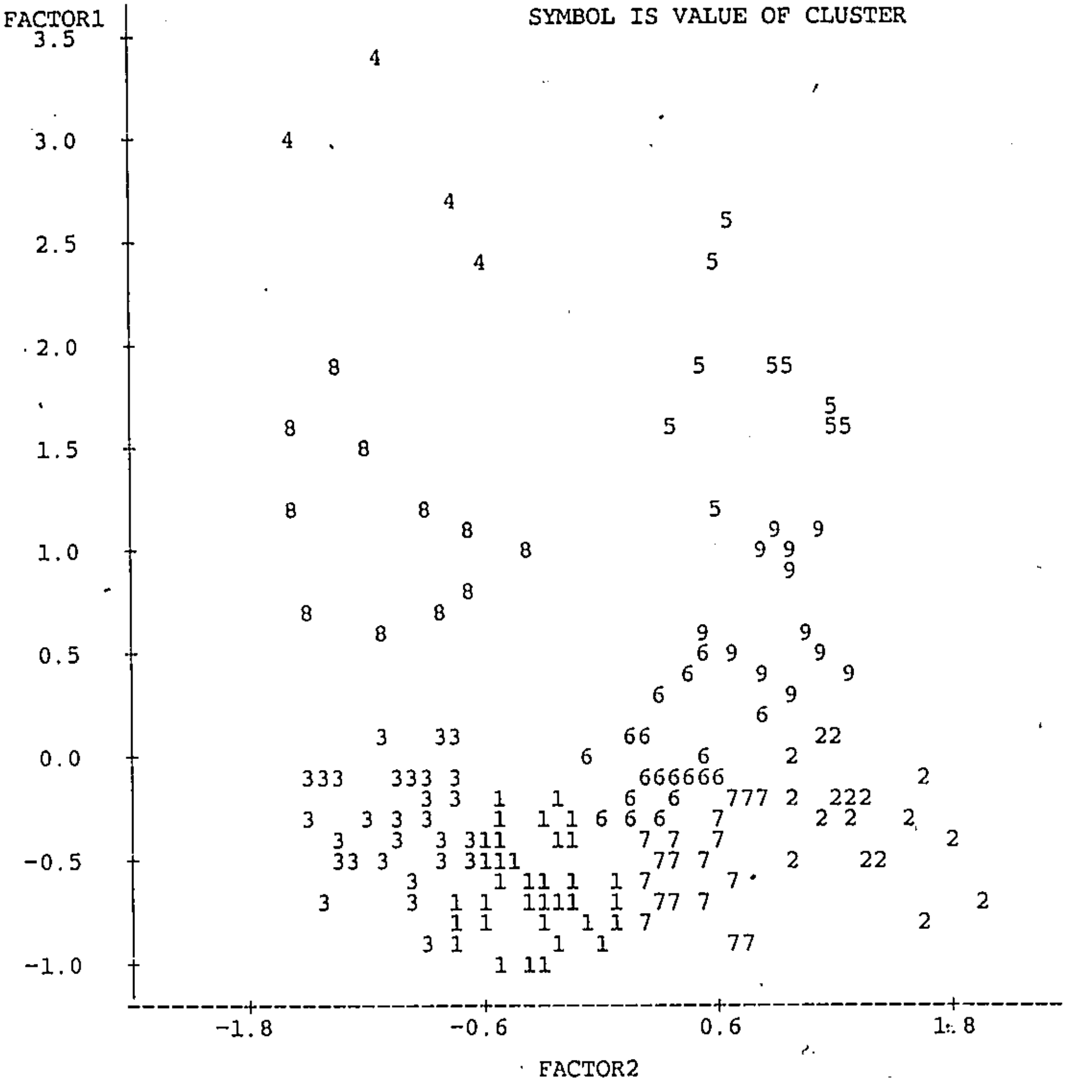
7.1.2 First Clustering

Following several clustering trials with anywhere from five to twelve clusters, a cluster number of nine appeared as the most appropriate. After several more trials with or without iterations and drifting, a final optimal solution of nine clusters obtained without drift and with only four iterations was chosen. This clustering solution best satisfied the criteria mentioned in the methodology, especially homogeneity and stability of the clusters. The nine groups are generally compact and quite well defined (fig. 5).

A canonical discriminant analysis was performed as a form of verification to see whether the dispersion pattern would be appraised in a way similar to that of principal factor analysis given the chosen clusters. The two canonical axes which best differentiate between clusters are, with minor modifications, the same as were obtained after rotation using principal factor analysis (table 5).
The reconstructed dispersion pattern is also very similar (fig. 6).

A cluster by cluster univariate analysis was performed to better circumscribe their individual characteristics. The nature of the clusters is defined in table 6.

Two types of clusters are now readily apparent: those which can be qualified of "pure" types and those which occupy intermediate positions between the pure types and can therefore be qualified of "intermediate" types. For the moment, we will purposefully refrain from using a terminology which implies taxonomical relationships. The specimens found in clusters 2, 3 and 4 are clearly representative of three different pure types. Cluster 2 is composed of specimens which typically have leaves 2 to 2.5 times longer than wide, with many deep indentations (3 pairs per 4mm of leaf length, on average) and numerous branched hairs on the lower midvein but no other gland type. Cluster 3, being at the opposite extremity of factor 2, is exactly the opposite of cluster 2 with respect to crenation, indentation, relative leaf size and branched density: its specimens have very few



NOTE: 19 OBS HIDDEN

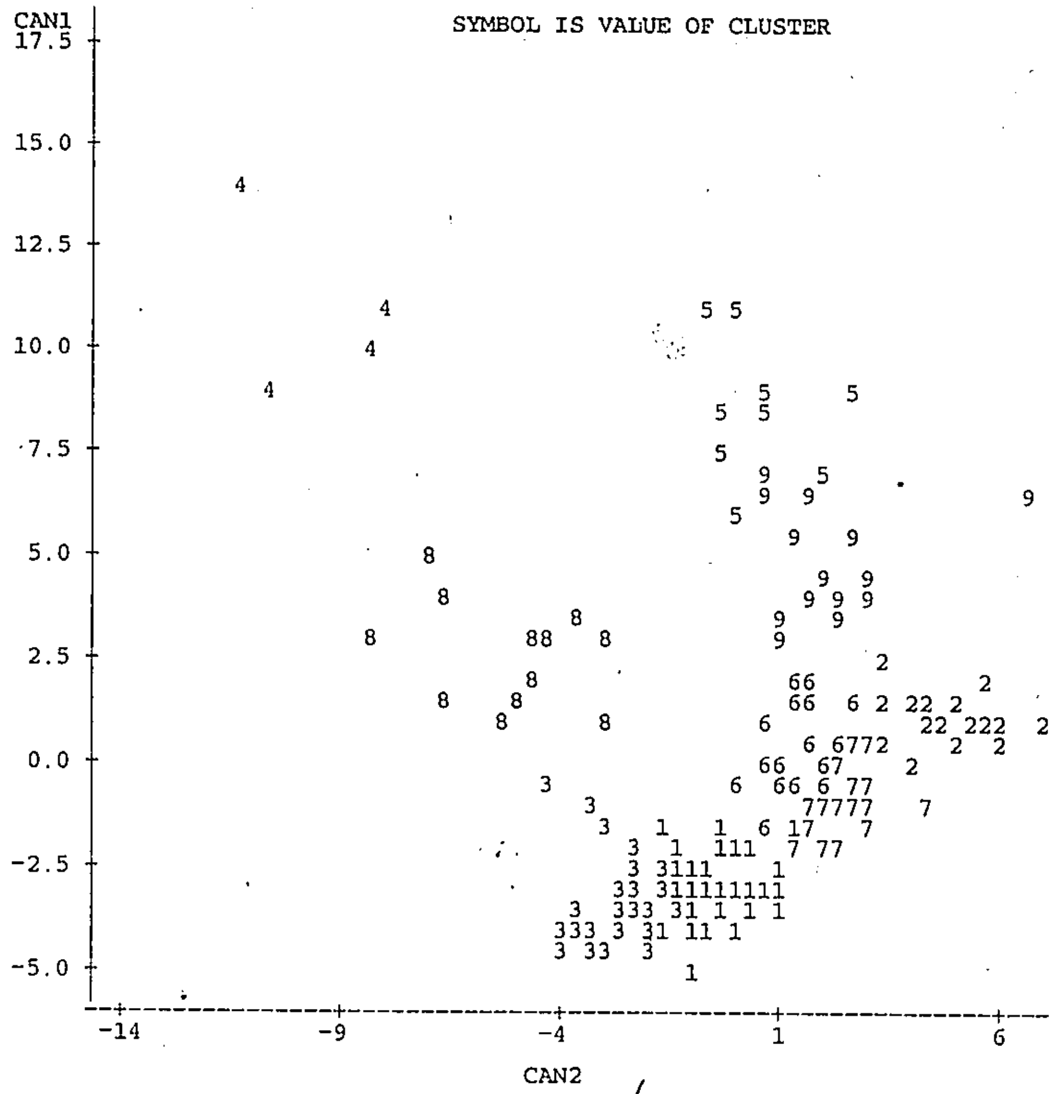
Figure 5: Plot of Principal Factors 1 and 2 with Cluster Membership

Table 5: Contribution of each Variable to the First 2 Canonical Axes

VARIABLE	STANDARDIZED CANONICAL COEFFICIENTS	
	CAN1	CAN2
PEDUNCLE	0.1390	0.2724
LOWSESSI	1.4619	-0.1577
UPSTALK	0.1193	0.1588
LOWSTALK	1.8171	-1.3684
LOWBRANC	0.2172	0.4953
UPSESS	0.5286	-0.3788
RELASIZE	-0.4449	-1.0883
RELINDEN	1.2153	1.3296
RELACREN	0.1165	0.4092
PETLENMM	-0.0368	0.0678
RELABASE	-0.2337	0.4579

indentations --which on average are not as deep--, no branched hairs and are typically 3 to 4 times as long as broad. On the other hand, their very similar positions along factor 1 means that, like cluster 2, cluster 3 has none of the other gland types. Finally, cluster 4 is typified by the presence of stalked and sessile glands, the former on the lower midvein and the latter also on the upper leaf surface. The leaves are crenated, but more coarsely so (average of 2 pairs of indentations per 5 mm), and not as deeply as those of cluster 2 specimens. The leaves are relatively narrow: 3.5 to 4 times longer than wide.

Clusters 1, 6, 7 and 8 occupy intermediate positions between the clusters representing the relatively pure types (fig. 5) and typically possess characteristics which appear to be the result of interbreeding or hybridization between pure types. Cluster 8 specimens exhibit average characteristics which are mainly a mix of those found in clusters 3 and 4: some stalked and sessile glands, very few indentations if any (average of 1 pair per 5mm), leaves 4 to 4.5 times longer than wide, mostly no branched hairs. However, it contains a few specimens which indicate a certain influence of type 2 since they possess some



NOTE: 37 OBS HIDDEN

Figure 6: Plot of Canonical Axes 1 and 2 with Cluster Membership

Table 6: Cluster Characteristics

Clusters for the first clustering procedure. Range of values for the more important variables of factors 1 and 2. Means (mn) or medians (md) are provided where appropriate. The first number corresponds to the CLUSTER NUMBER. The variable RELACREN was not included since it only serves to differentiate clusters 2 and 9 (medians= 0.2) from the rest (medians= 0.1).

	FACTOR 1			FACTOR 2		
	LOW-STALK	LOW-SESSI	UP-SESS	REL-INDEN	REL-ASIZE	LOW-BRANC
1)	0	0 or v.few	0 or v.few	0-1.1 md=0.2	1.9-4.1 mn=2.8	0; 7-26 bimodal
2)	0	0 or v.few	0 or v.few	1.2-2.0 mn=1.5	1.6-2.7 mn=2.2	7-25 mn=15
3)	0	0 or v.few	0 or v.few	0-0.7 md=0.1	2.6-4.7 mn=3.6	0
4)	11-19 md=16.5	5-11 md=9	3-18 md=10.5	0.6-1.1 md=0.8	3.3-4.4 mn=3.8	0-3 md=0
5)	0-9 md=5.5	5-33 md=18	3-15 md=6.5	0.9-1.7 mn=1.3	1.5-3.0 md=2.5	5-24 mn=14
6)	0 or v.few	0-8 md=2	0-12 md=2	0.5-1.6 mn=1.0	2.2-3.2 md=2.6	0-18 mn=10
7)	0	0-6 md=0	0-8 md=1	0.5-1.3 md=1.0	2.0-3.2 md=2.4	0;10-23 bimodal
8)	0-7 md=5	3-15 md=9	1-14 md=5	0-0.8 mn=0.4	3.0-4.9 mn=3.7	0-6 md=0
9)	0-8 md=2	1-17 md=8	0-14 md=4	1.0-2.6 md=1.4	1.6-3.2 mn=2.4	1-28 md=15.5

branched hairs. The lack of a more continuous gradient between cluster 8 and clusters 1 or 6 may be due to the low numbers, but this appears unlikely: at least a few specimens would occupy a more intermediate position.

Clusters 1, 6 and 7 fill the gap between clusters 2 and 3 (fig. 5). This gradient includes a large proportion of the specimens measured (table 7): this is by far the most common form of interbreeding.

Table 7: Summary of Cluster Information

Given are: frequency, radius of cluster, nearest cluster and means for factors 1 and 2.

CLUSTER	FREQ	RADIUS	NEAR	FACTOR1	FACTOR2
1	46	0.49179	3	-0.62336	-0.3249
2	19	0.75824	7	-0.27487	1.3265
3	31	0.58813	1	-0.31587	-1.0548
4	4	0.66331	8	2.88811	-1.0035
5	10	0.85195	9	1.82775	0.8245
6	21	0.58945	7	-0.00652	0.3384
7	18	0.51086	6	-0.53293	0.5035
8	12	0.89812	3	1.08791	-1.0458
9	14	1.24115	6	0.75243	1.0423

Clusters 1 and 7 are unambiguously located directly along and at the same level on the 3-2 gradient as clusters 2 and 3 (fig.5), an indication that none or very few stalked or sessile glands are found on the specimens. Their contents are somewhat mixed in nature with respect to the variables represented in factor 2 because of properties inherent to the principal factor model. The intermediate clusters are not necessarily composed only of hybrids. Note in particular the bimodality of LOWBRANC in clusters 1 and 7 (table 6). The combination of values for all the variables defines the position of each specimen along factor 2. Although the extremes are well differentiated by factor 2, namely the specimens of clusters 2 and 3, in an intermediate specimen, one extreme value can result in a factor 2 coordinate which does not necessarily reflect the overall nature of the specimen as can be appraised when a certain discrimination is applied with respect to the combination of values. The specimens of clusters 1, 6 and 7 are re-examined in a second principal factor analysis followed by a second clustering. Suffice to say that, collectively, they encompass the specimens which generally demonstrate characteristics which are typically intermediate to those of clusters 2 and 3.

While clusters 1 and 7 are directly along the gradient of variation between 2 and 3, cluster 6 occupies a position which, albeit similar to that of cluster 7 with respect to factor 2, also demonstrates a different hybridization pattern by its position along factor 1. The tendency is toward cluster 9 instead of 2, indicating the appearance of sessile glands mainly in the definition of this group (table 6). The pattern is all the more interesting since it does not exist at the opposite end of the factor 2 gradient between clusters 2 and 3: cluster 1 is the only hybrid group which neighbors cluster 3 along that gradient.

Cluster 9, although intermediate by its position (fig.5), appears to have a different status because of the presence of cluster 6 and the characteristics of cluster 5 described below. It is certainly closely associated to cluster 2 from which it differs only by the presence of stalked and, more importantly, sessile glands (table 6). The type it represents may well have a more independent status than any other intermediate type and form quite distinct demes. The presence in cluster 5 of specimens which seem to indicate by their phenotype that hybridization between types 9 and 4 occurs and produces characteristic hybrids with extreme sessile gland density supports this hypothesis.

Despite its seemingly extreme position (fig.5) and apparently distant relationship to cluster 4 --an artefact of the factor analysis-- cluster 5 is truly in an intermediate position between clusters 2 and 4, with specimens typically having slightly coarser crenation than 2 and, much like cluster 8, several stalked glands albeit an average of twice as many sessile glands on the lower midvein. There is however a peculiar distribution of values for the variables LOWBRANC and LOWSESSI. In spite of the apparent nature of the cluster as an intermediate between the types 2 and 4, the value of LOWBRANC is constantly high, almost as high as that of type 2 although type 4 typically has no branched hairs. LOWSESSI reaches its highest values in this cluster, a possible indication of the additive nature of that particular gland character for the type 9-4 hybrids (table 6). Thus, cluster 5 has characteristics which indicate a hybridization gradient between clusters 2 and 4: the specimens it contains are all intermediate between 2 and 4, although more or less closely associated to clusters 2, 9 and 4.

7.1.3 Second Principal Factor Analysis

This second factor analysis was performed on data extracted from the matrix of 175 specimens and 18 variables. Extracted were those observations which were assigned to clusters 1, 6 or 7 of the first clustering. The reason for this was the lack of homogeneity of those clusters, as described in the previous section, which makes their interpretation difficult and prevents the recognition of general characteristics for each one.

Two principal factors were retained in the final version and account for 96% of the total covariation (table 8). Ten variables were involved : RELINDEN, PEDUNCLE, RELASIZE, RELABASE, PETLENMM, RELACREN, LOWSESSI, LOWSTALK, LOWBRANC and UPSESS.

Table 8: Contribution of the Principal Factors to Covariation

	PRINCIPAL	FACTORS
	A	B
EIGENVALUE	1.433955	1.028955
DIFFERENCE	0.405000	0.419737
PROPORTION	0.5591	0.4012
CUMULATIVE	0.5591	0.9603

As done previously, the final choice was based on a maximization of Kaiser's overall measure of sampling adequacy and sampling adequacy for each variable. Because the extracted data has only 95 observations, Kaiser's measure is low, but acceptable (MSA= 0.54). Rotations did not improve the factor solution. Factor A has two major contributing variables: RELACREN and RELINDEN. Both are positive contributors (table 9). RELINDEN and LOWBRANC are the important variables negatively associated to factor B while RELABASE and PETLENMM are positively associated to it (table 9).

Table 9: Factor Pattern for Principal Factors A and B

```
               FACTOR A   FACTOR B

  RELACREN     0.70208    0.01124
  RELINDEN     0.61661   -0.32437
  LOWSESSI     0.41386   -0.30269
  PEDUNCLE     0.28460    0.08851
  LOWSTALK     0.25388   -0.20755
  RELABASE     0.17119    0.55807
  PETLENMM     0.09438    0.43339
  RELASIZE     0.30739    0.33023
  UPSESS       0.07558   -0.18529
  LOWBRANC    -0.32510   -0.37205

VARIANCE EXPLAINED BY EACH FACTOR

          FACTOR A   FACTOR B
          1.433955   1.028955
```

The particular importance of RELINDEN for both factors is to be noted as is that of LOWBRANC for factor B since these two variables were significant in the first factor analysis as well. Overall, they are two strongly discriminating variables.

Factor A is mostly defined in terms of crenation while factor B is defined in terms of crenation, shape of leaf base and branched hair density. Since the extracted observations were, in the first factor analysis, in a position which effectively eliminated the three other variables for gland density as discriminating variables, the result of the second analysis is not surprising.

The dispersion diagram for factors A and B (fig. 7) is without distinct clumps of observations. Certain small groups are visible, but since the observations were quite continuously distributed along factor 2 in the first analysis, the continuous nature of the dispersion was to be expected. Nevertheless, the shape of the distribution suggests a possible division at the narrower central section and a third group below the center.

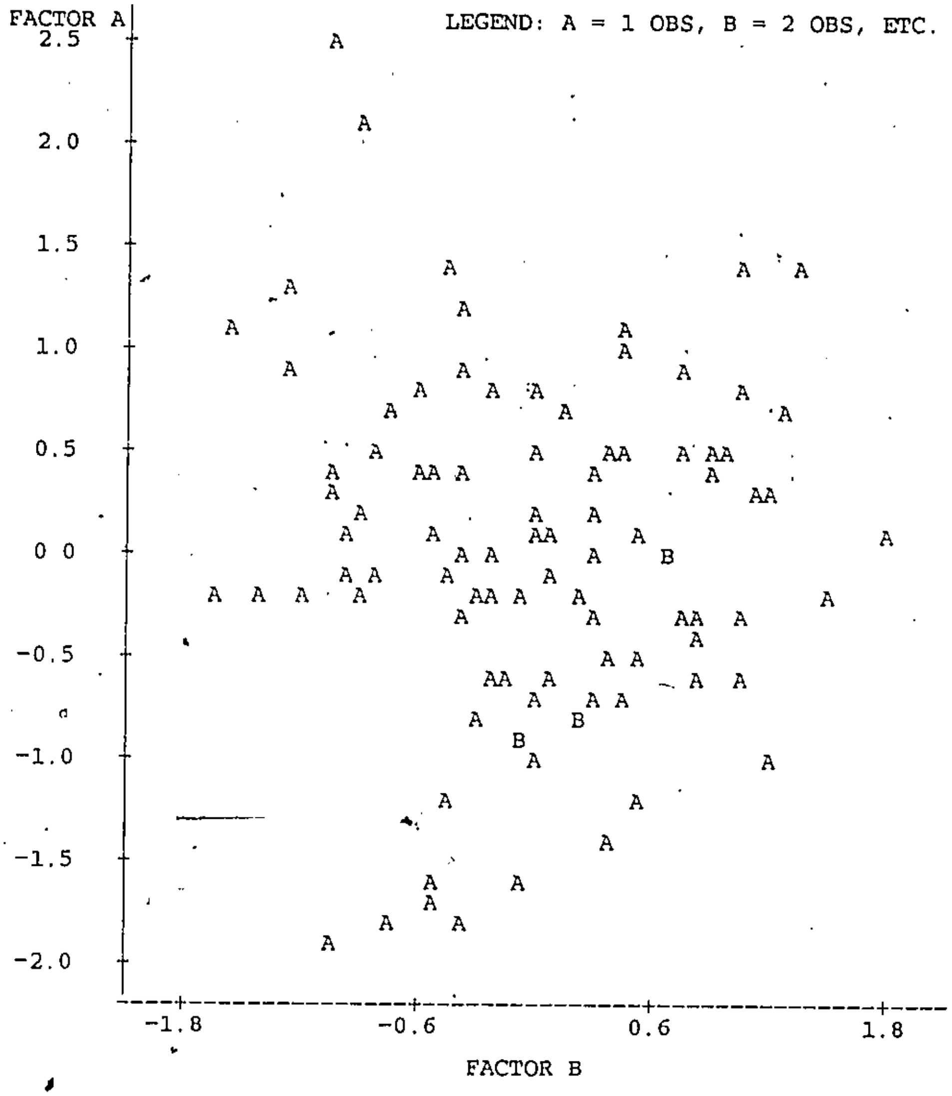


Figure 7: Dispersion Diagram for Factors A and B

7.1.4 Second Clustering

Clustering trials were made for two to five clusters. The five cluster solution best satisfied the homogeneity and stability criteria, when combined to a drifting option of the cluster seeds for two iterations. Four of the five groups contain similar numbers of observations (table 10).

Table 10: Summary of Clusters

Given are: frequency, radius of cluster, nearest cluster and means for factors A and B.

CLUSTER	FREQ	RADIUS	NEAR	FACTOR A MEAN	FACTOR B MEAN
A	23	1.30418	4	-1.0090	-0.16717
B	2	0.16945	3	2.3025	-0.95185
C	28	1.10054	5	0.3775	-0.79761
D	25	1.16910	5	-0.1861	0.67154
E	17	0.81457	4	0.7461	0.66431

The five groups have quite distinct characteristics in spite of the continuous nature of the dispersion (table 11). Cluster A shows a large number of branched hairs but very few crenations: its characteristics undoubtedly place it halfway between clusters 2 and 3 of the first clustering. Cluster B only regroups two outliers, a case of extreme crenation but few branched hairs. Cluster C definitely has strong affinities with cluster 2: its specimens have several crenations per leaf (at least 1 pair per 4mm) and several branched hairs. Cluster D shows the opposite of C, with few crenations and very few branched hairs, if any. These characteristics relate it closely to cluster 3. Finally, cluster E has a pattern of characteristics opposite to that of A: its members have few branched hairs, if any, but quite a few crenations, in fact almost as many as the members of cluster C. We therefore have two pairs of opposed clusters representing all four combinations of extremes for the two variables RELINDEN and LOWBRANC (fig. 8).

Table 11: Cluster Characteristics

Range of values and median for the more important variables of Factors A and B of the second factor analysis.

CLUSTER	RELACREN	RELINDEN	LOWBRANC	RELABASE	PETLENMM
A	0-0.1 md=0.1	0-0.8 md=0.1	0-26 md=14	0.1-0.6 md=0.5	0-0.7 md=0.2
B	0.2	1.4	1;2	0.6	0;0.1
C	0.1-0.2 md=0.1	0.5-2.0 md=1.0	0-18 md=12	0.1-0.6 md=0.4	0-0.7 md=0
D	0-0.2 md=0.1	0.1-1.1 md=0.3	0-16 md=0	0.3-1.0 md=0.6	0-1.3 md=0.3
E	0.1-0.3 md=0.2	0.3-1.3 md=0.9	0-12 md=0	0.3-0.8 md=0.6	0-1.4 md=0.6

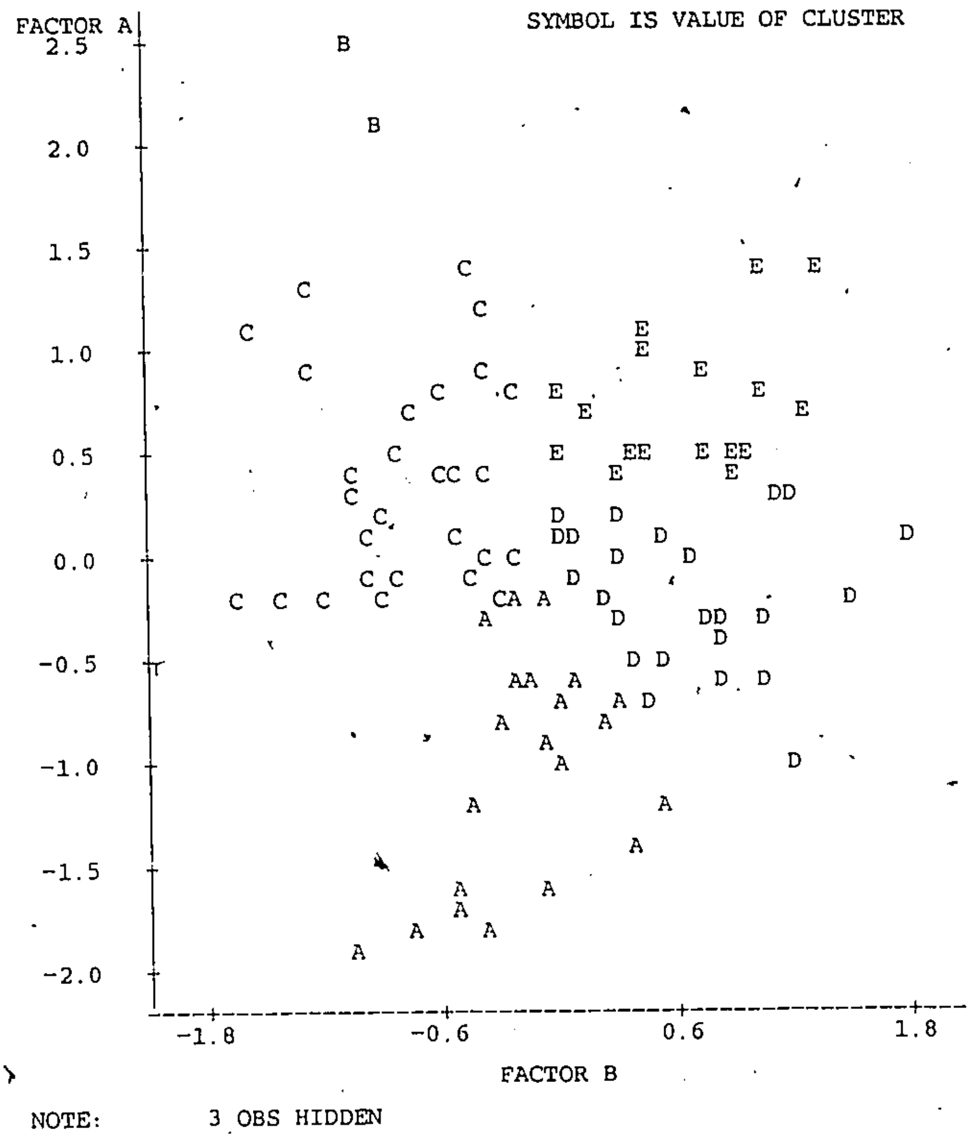


Figure 8: Plot of Factors A and B with Cluster Membership

7.2 Identification and Geographic Distribution

Two discriminant identification functions were obtained separately: the first one based on the results of the cluster analysis of all of the 175 specimens for which 14 variables were measured, and the second one based on that of the extracted data belonging initially to clusters 1, 6 and 7. Each identification function was then applied in turn to the matrix of the remainder of the specimen sample for which seven variables had been measured. The first identification function assigned each individual specimen to one of clusters 1 to 9. For those specimens assigned to clusters 1, 6 or 7, the second identification function assigned membership to one of clusters A to E.

The identification variable DRYAS combines the information which resulted from the two identification functions to describe the combination of types found at any given site. The distributional information can thus be used in the ecological analysis, the results of which are detailed in the next section. The distribution pattern for each value of the DRYAS variable --11 in all-- is represented on the maps which follow (figs. 9-19). One striking feature of most distribution patterns illustrated is the seemingly important role of the ranges.

Type 2 is clearly present throughout the region (fig. 9). When present, it is generally an important contributor to the total vegetal cover of the community.

Type 3 is strikingly absent from the Ruby Range in our sample. Its restriction to the Kluane Ranges is possibly related to geology (fig.10).

Type 4 is also mainly found in the Kluane Ranges. However, evidence of its presence has been found at one location in the Ruby Range. This important difference with type 3 possibly indicates that the Shakwak Trench is not an unsurmountable obstacle, if indeed the source of the Ruby Range specimens is the Kluane Ranges (fig. 11). The distri-

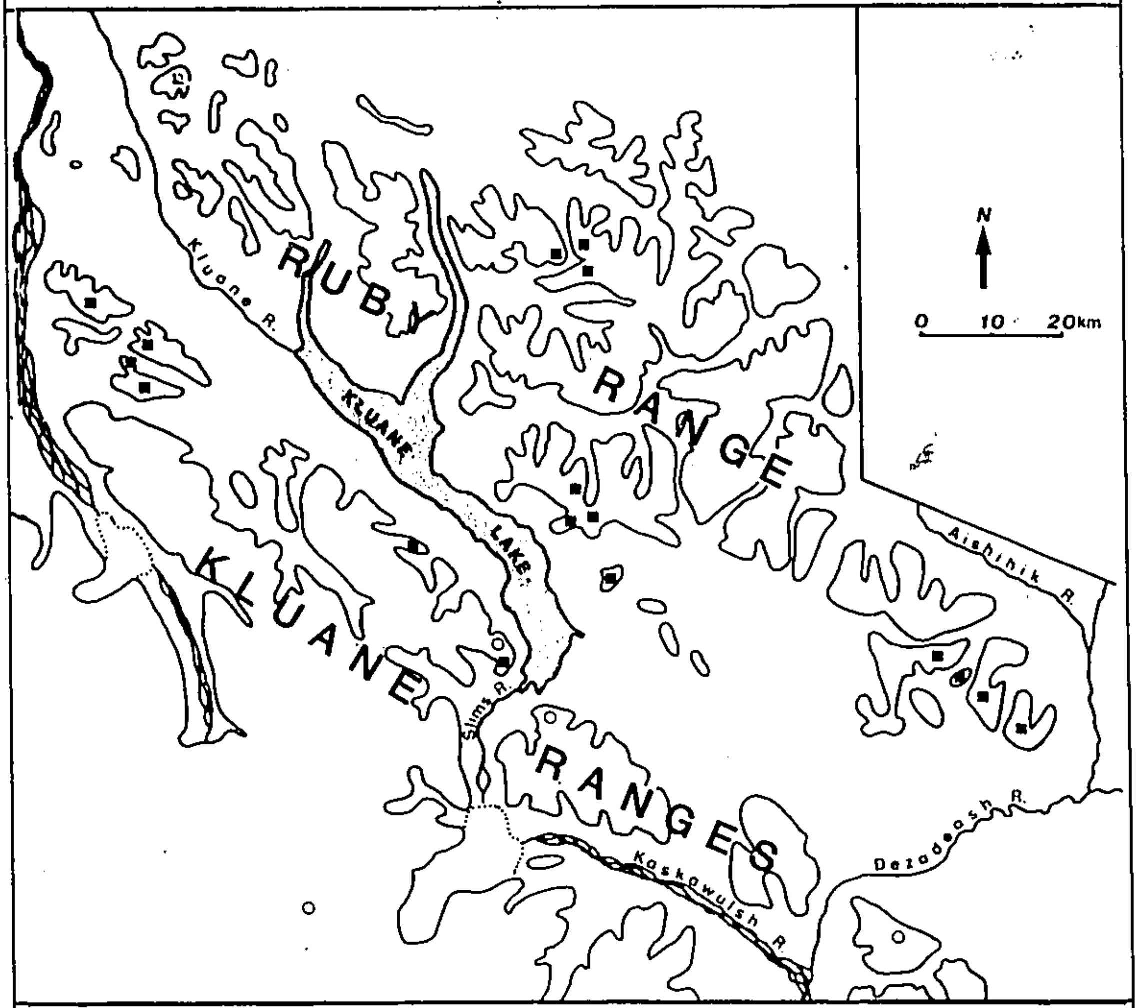


Figure 9: Occurrences of type 2. Distribution of the sampling areas where type 2 exclusively (black square), or a combination of types which includes type 2 (white circle) was recorded for at least one individual site.

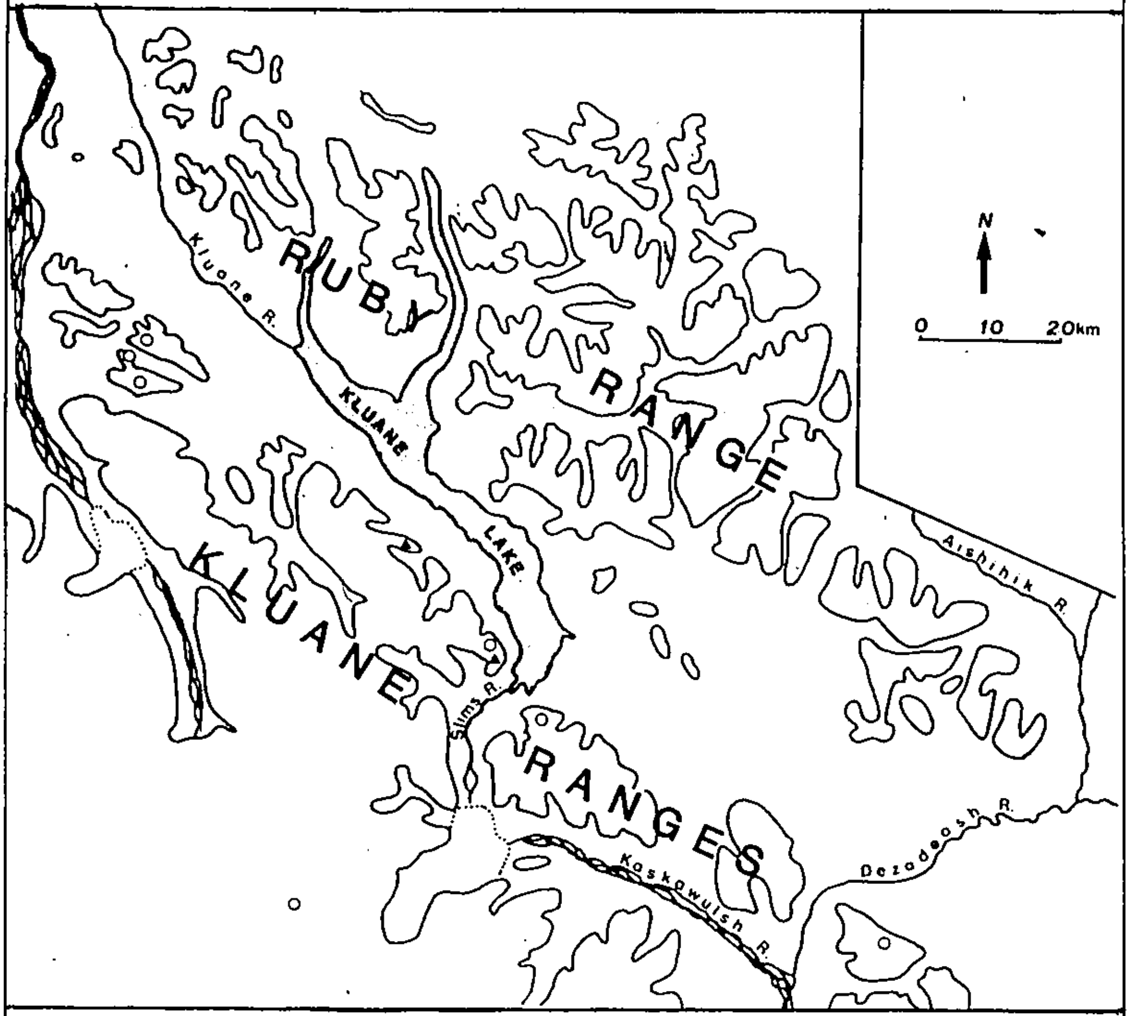


Figure 10: Occurrences of type 3. Distribution of the sampling areas where type 3 exclusively (black triangle), or a combination of types which includes type 3 (white circle) was recorded for at least one individual site.

bution is based on hybridization evidence mainly since the frequency of type 4 is such that it is rarely found by itself (table 7). The Outpost meadows have particularly abundant evidence of the presence of type 4, direct and indirect. Hybridization in that location between type 4 and types 2 and 3 is particularly common and has been found to sometimes exist without the contiguous presence of 2-3 hybridization (fig.12).

Evidence of the presence of type 9 was obtained throughout the Kluane Ranges (fig. 13). Type 9 is also present at several sites in the Ruby Range, but its seeming absence from the northern part of the range may support the hypothesis that type 9 has a distinct status and is not just a hybrid closely related to type 2.

Because the types 2 and 3 only coexist in the Kluane Ranges, it is also there that hybridization occurs. One apparent exception is a single hybrid specimen found at the Tincup Lake location in the Ruby Range. However, the specimen in question is clearly more closely related to type 2 than type 3 in morphology. It could be an indication of the very scarce presence of type 2 in the area but may well be an aberrant specimen (fig. 14).

Hybridization between types 2, 9 and 4 is quite common in spite of relatively low frequency of type 4. Chorologically, it follows the same pattern as the map of type 4 distribution. Only in the Tincup Lake area of the Ruby Range have type 4 hybrids been found (fig. 15).

Hybridization between type 4 and type 3 is much more limited (fig. 16). Again, this is clearly related to the distribution patterns of the two parent species which seem to be mainly restricted to the Kluane Ranges. The combination of 4-3 and 3-2 hybridizations within a site indicates the extremely close contact which can locally exist between populations of all three pure types (fig.17). The same is true of 4-2 and 2-3 hybridizations (fig. 18). Surprisingly, the Auriol Range sample, while showing the presence of all three pure types, does not include any evidence of 4-3 hybridization (figs. 9, 10, 11, 17 and 18).

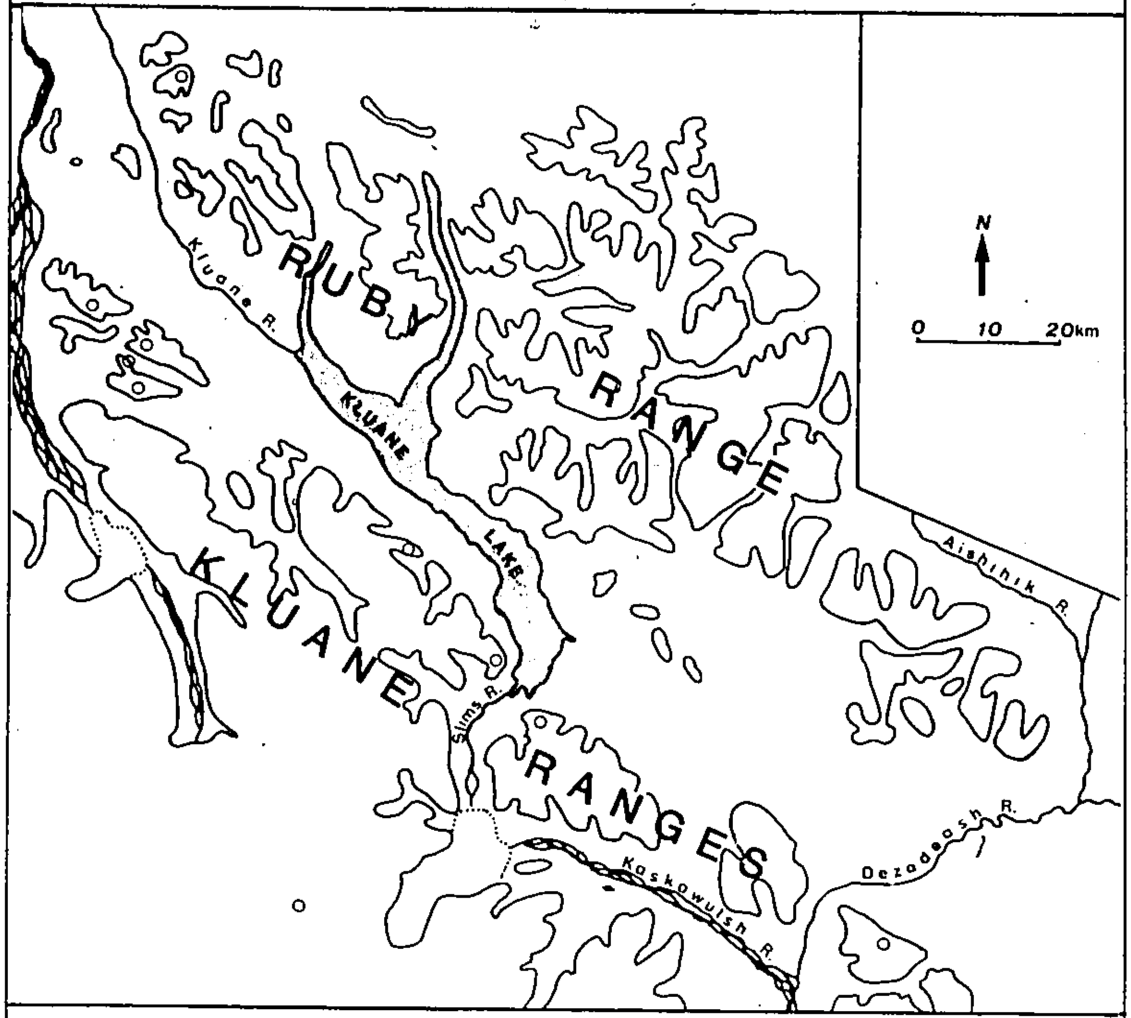


Figure 11: Occurrences of type 4. Distribution of the sampling areas where a combination of types which includes type 4 (white circle) was recorded for at least one individual site.

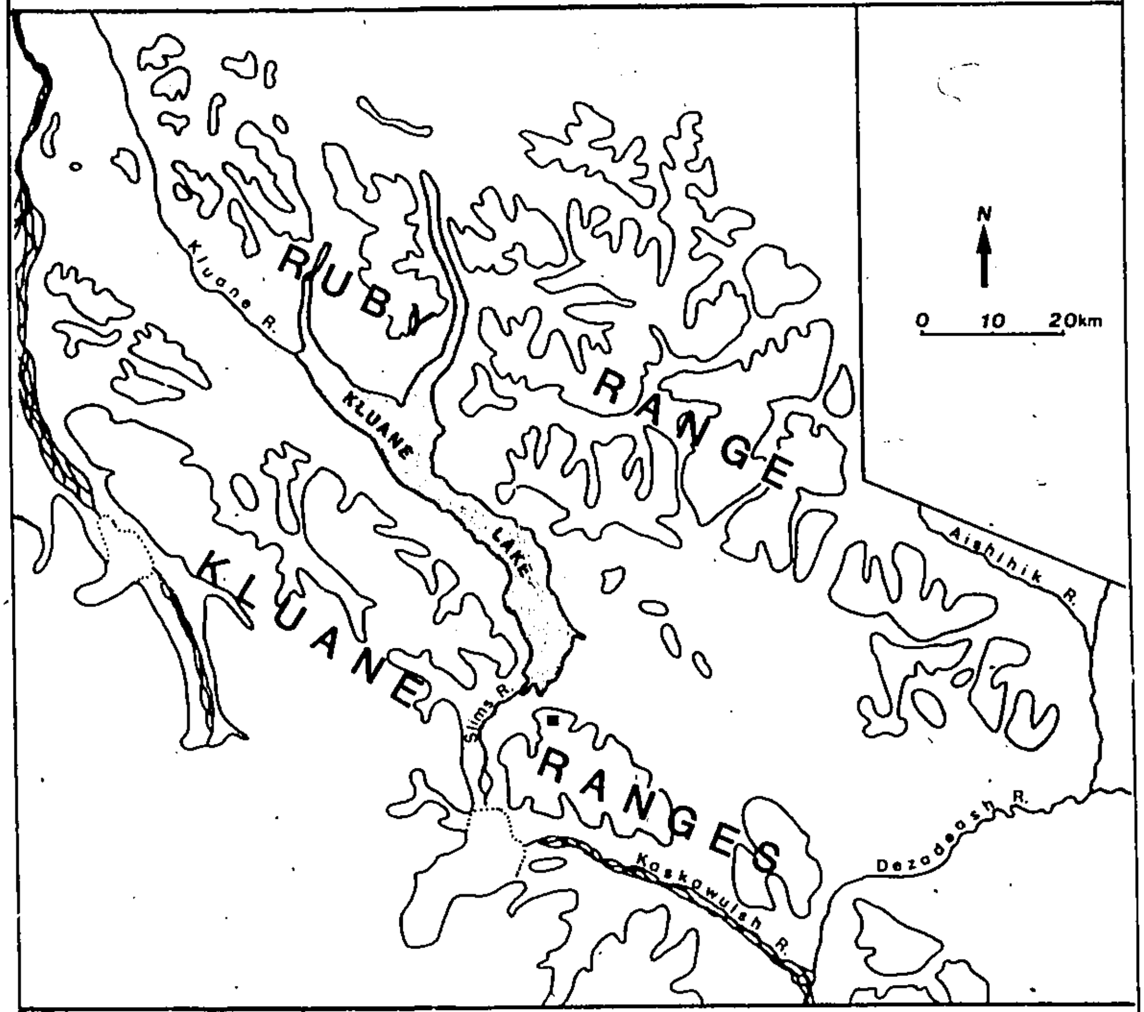


Figure 12: Occurrence of type 4-3 and 4-2 hybrids. Distribution of the sampling areas where hybridization between 4 and 3, and that between 4 and 2 (black square) were recorded for at least one individual site, in the absence of 2-3 hybrids.

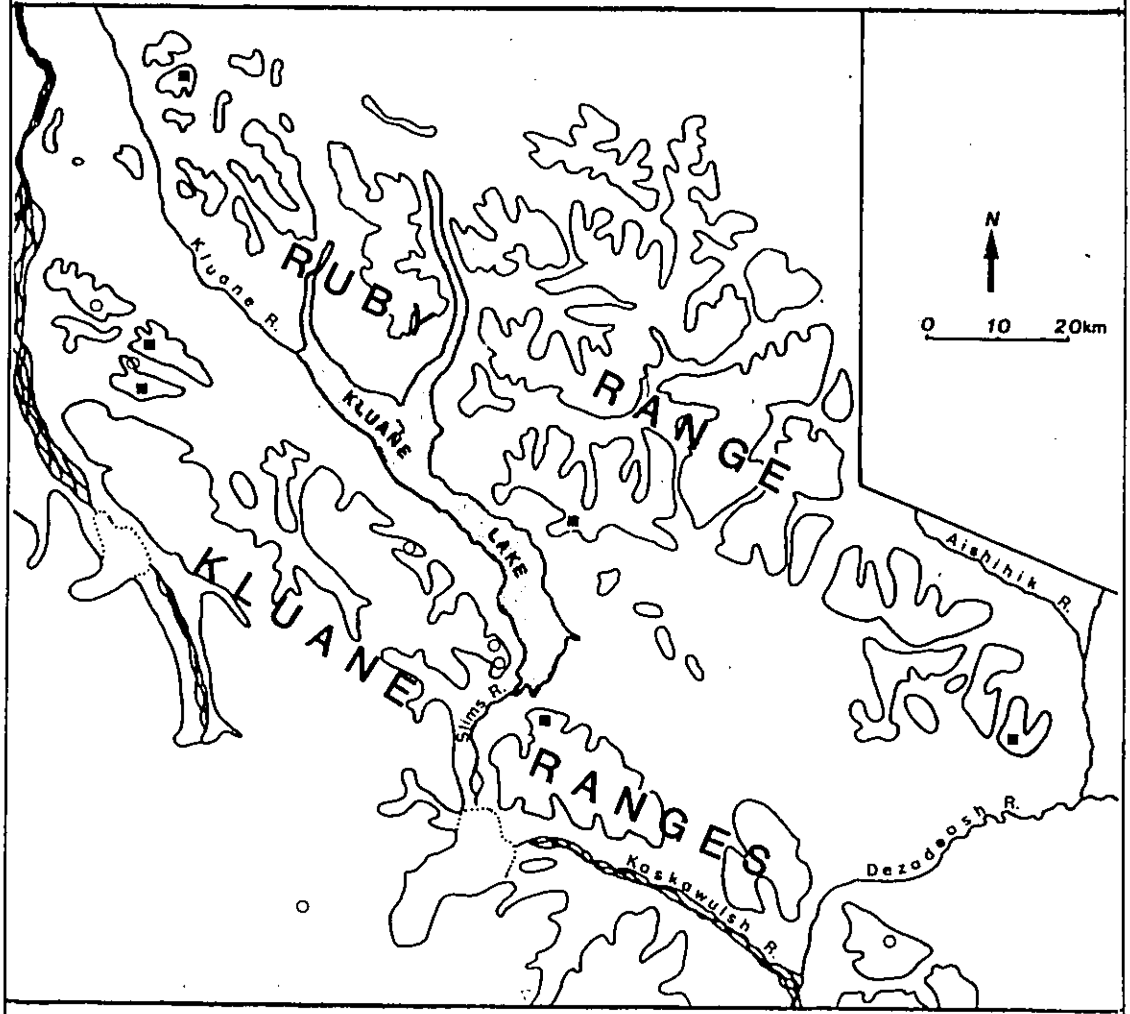


Figure 13: Occurrences of type 9. Distribution of the sampling areas where type 9 exclusively (black square), or a combination of types which includes type 9 (white circle) was recorded for at least one individual site.

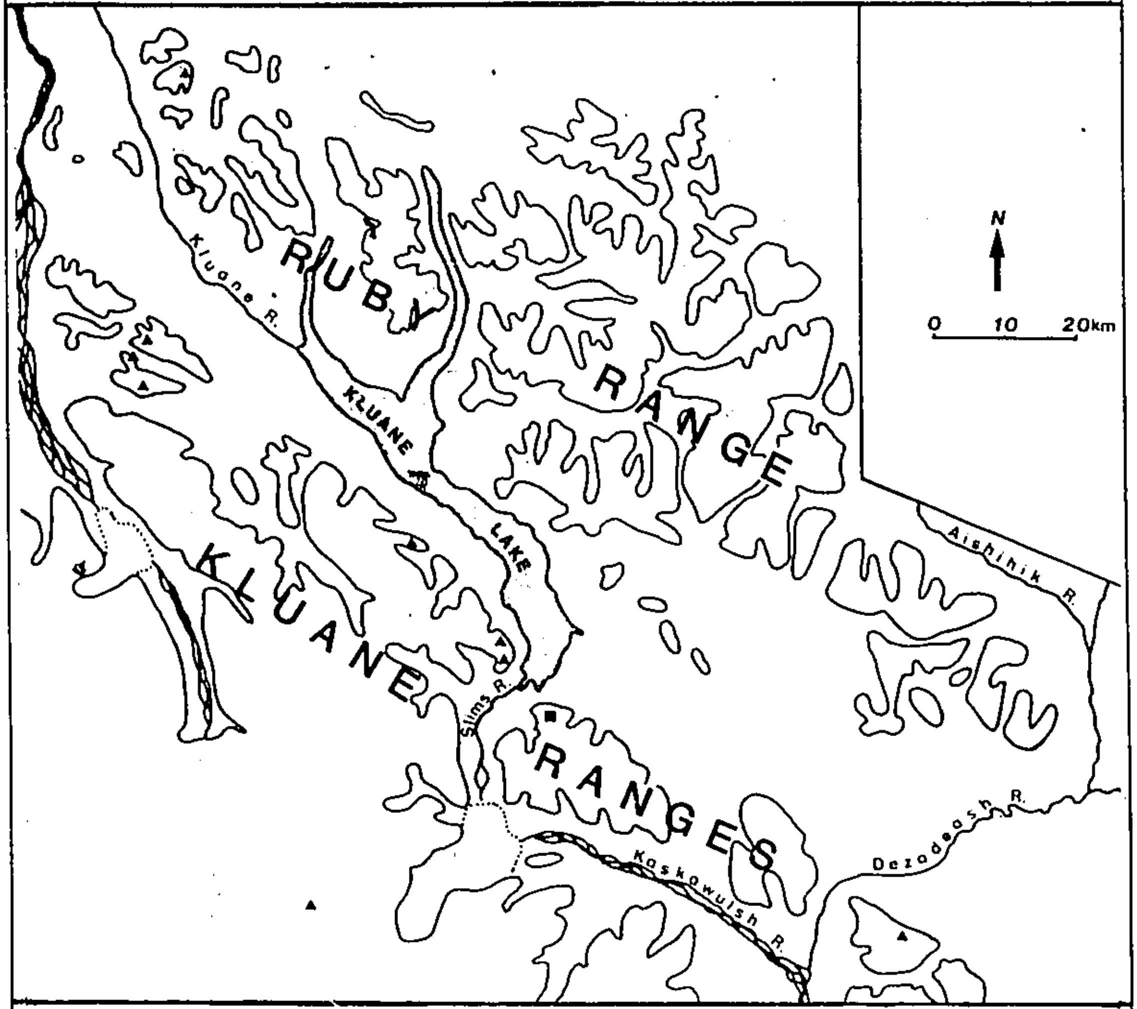


Figure 14: Occurrences of hybridization between types 2 and 3. Distribution of the sampling areas where hybridization exclusively between types 2 and 3 (black triangle) or hybridization which includes that between types 2 and 3 (black square) was recorded for at least one individual site.

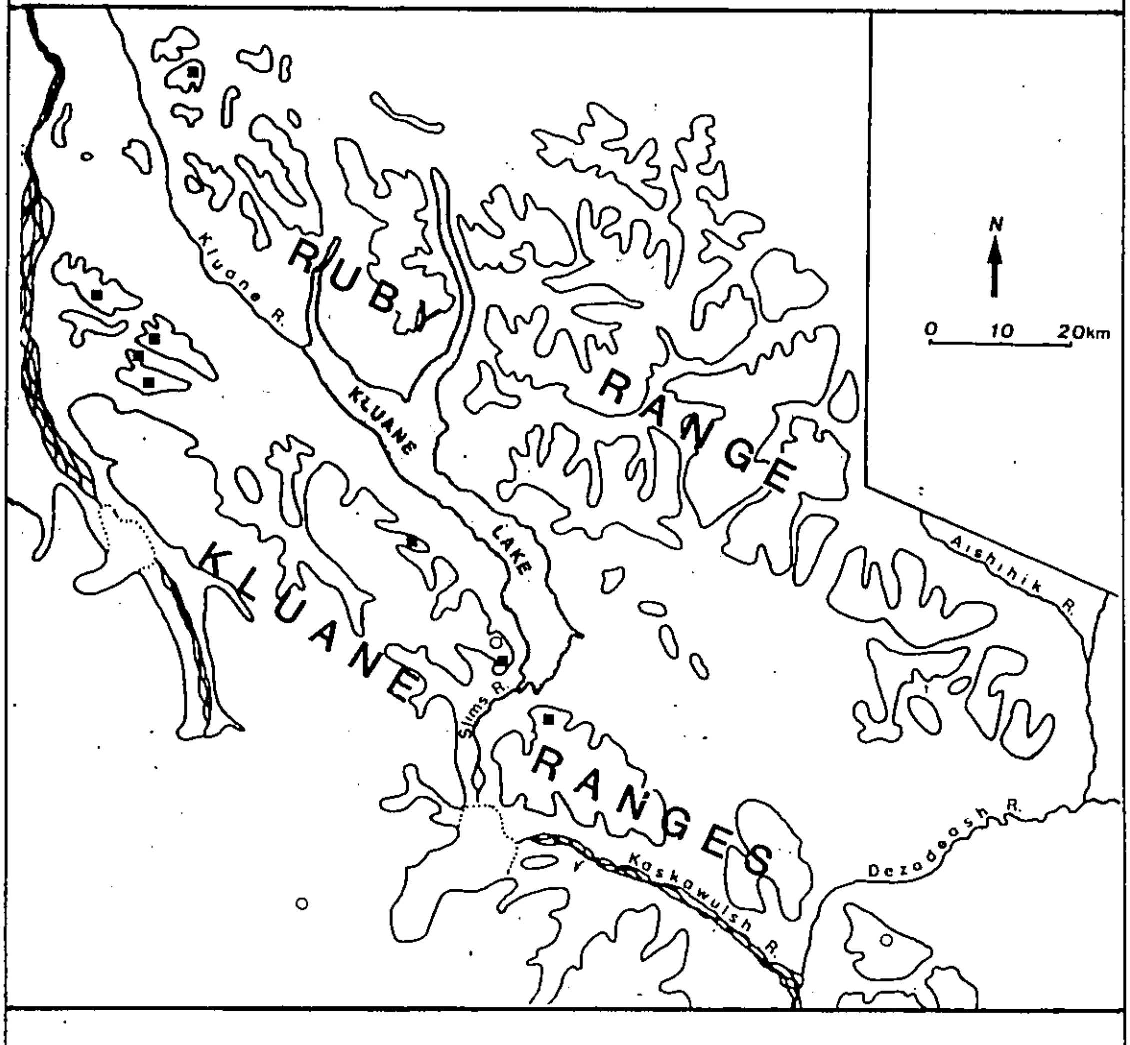


Figure 15: Occurrences of hybridization between types 2, 9 and 4. Distribution of the sampling areas where hybridization exclusively between types 2, 9 and 4 (black square) or hybridization which includes that between types 2, 9, 4 (white circle) was recorded for at least one individual site.

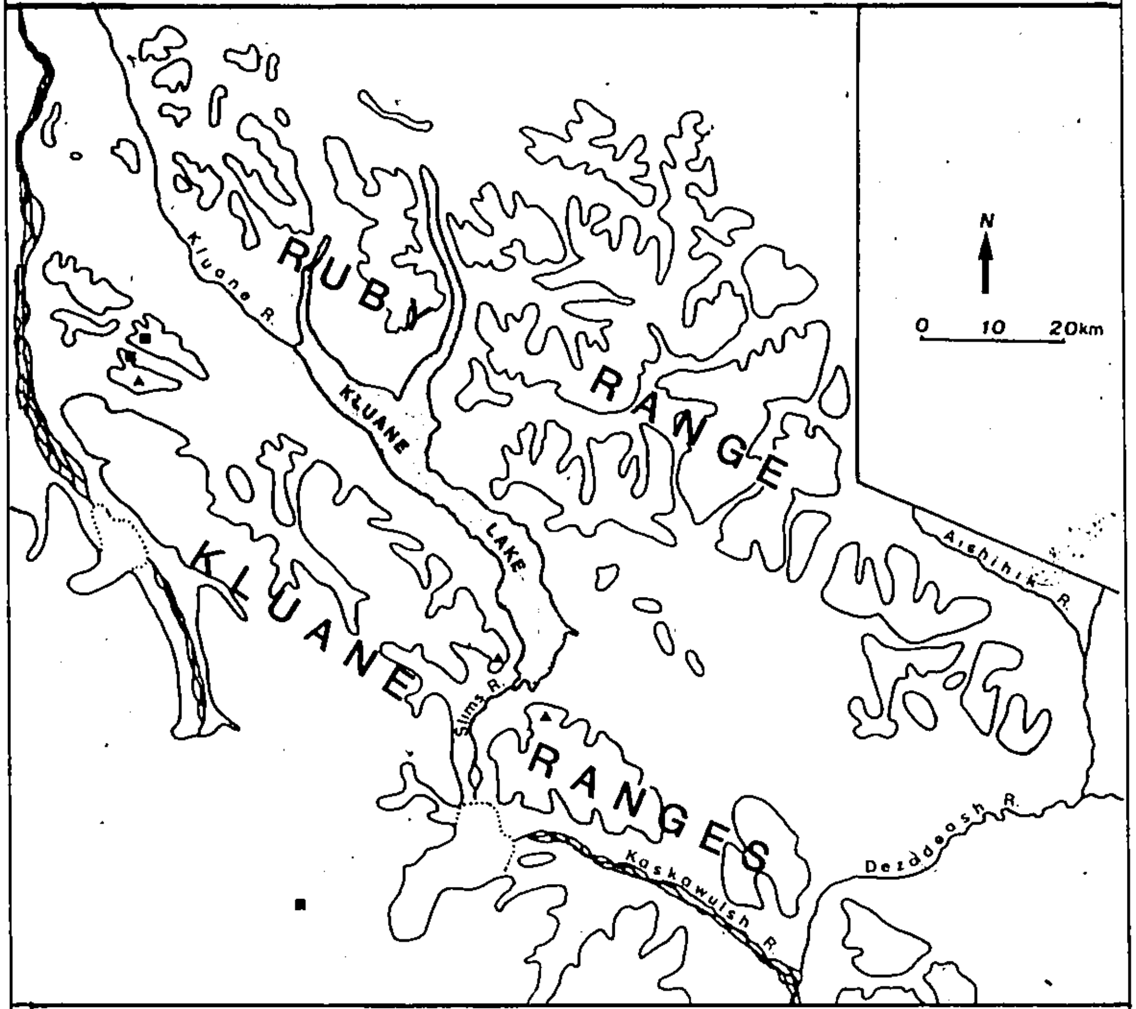


Figure 16: Occurrences of hybridization between types 3 and 4. Distribution of the sampling areas where hybridization exclusively between types 3 and 4 (black triangle) or hybridization which includes that between types 3 and 4 (black square) was recorded for at least one individual site.

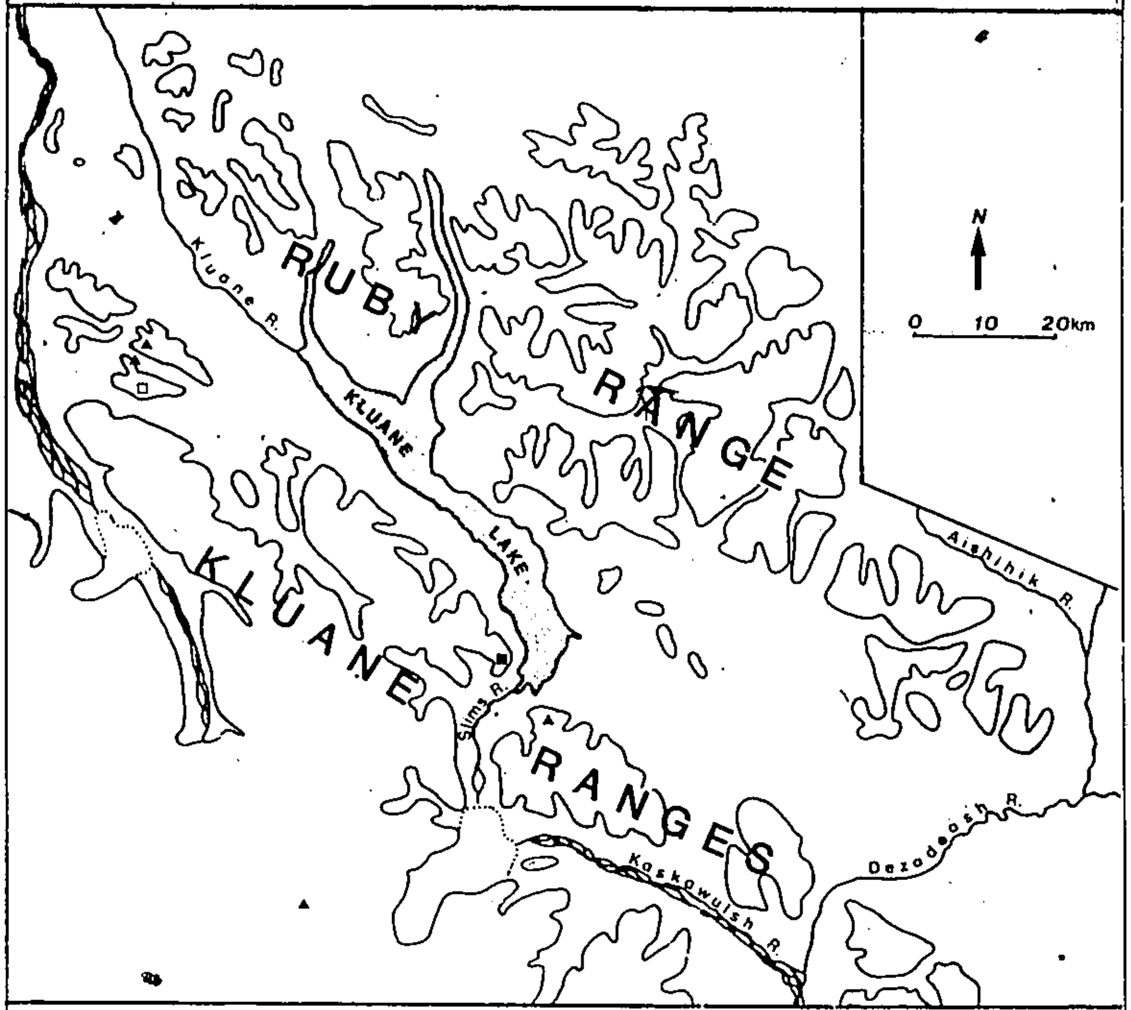


Figure 17: Occurrences of hybridization 2-3 and 3-4. Distribution of the sampling areas where hybridization exclusively between types 2 and 3, or 3 and 4 (black square), or hybridization which includes that between types 2, 3 and 4 (black triangle) was recorded for at least one individual site, or sampling areas where both types of hybridization occur, but at separate sites (white square).

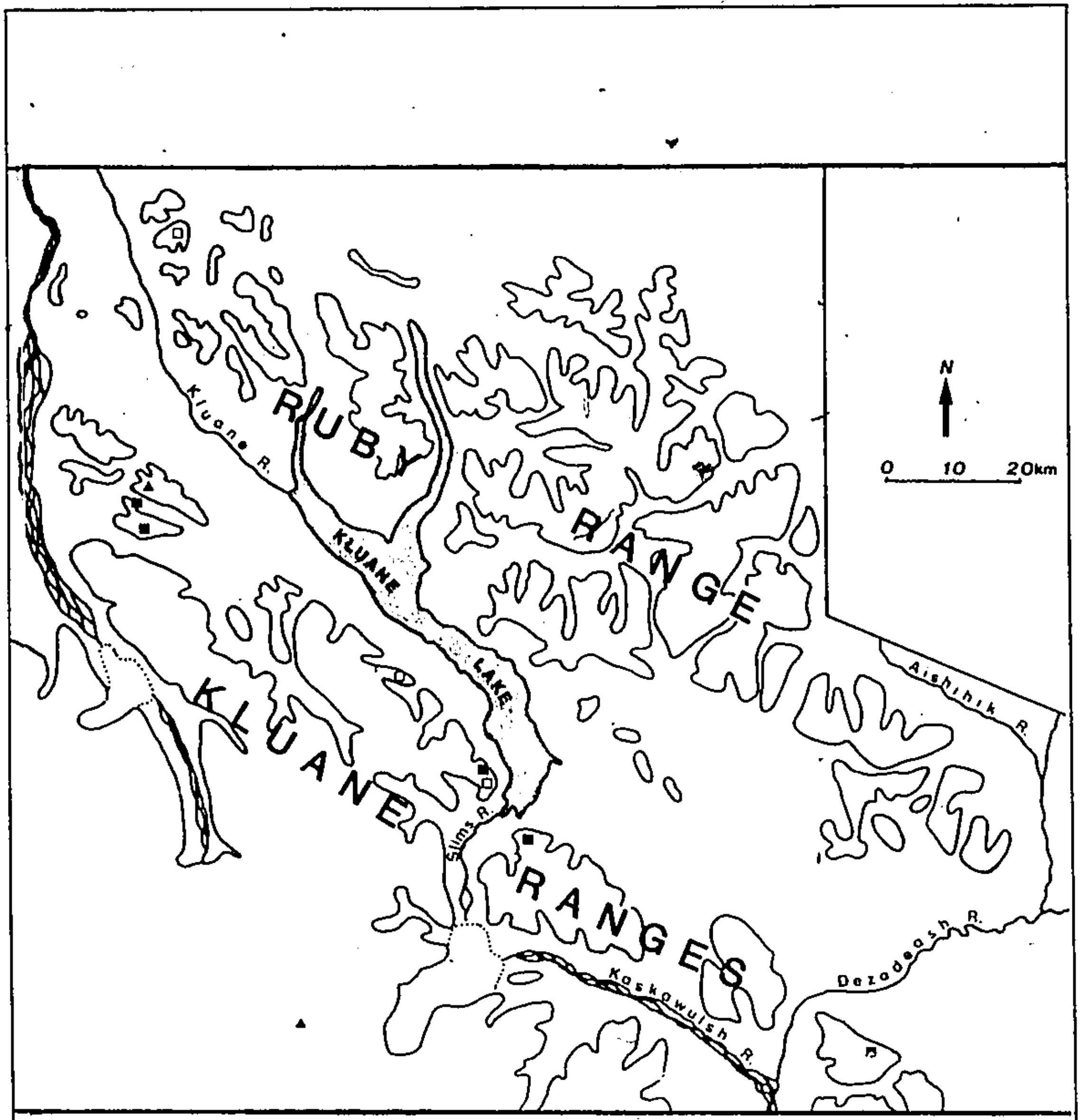


Figure 18: Occurrences of hybridization 3-2 and 2-4. Distribution of the sampling areas where hybridization exclusively between types 3 and 2, or 2 and 4 (black square) or hybridization which includes that between types 2, 3 and 4 (black triangle) was recorded for at least one individual site, or sampling areas where both types of hybridization are present, but at separate sites (white square).

Two areas of the Kluane Ranges and the Kaskawulsh location show the three forms of hybridization occurring within the confines of a particular site (fig. 19). This is clearly an indication of the close proximity of the pure populations in these areas. Both the Outpost and Quill Creek locations show this pattern of close contact between pure types. The Sheep Mountain and Tatamagouche Creek locations have all three pure types occurring also, but the occurrence of gene flow between the three is evidently not as common an event. Those two sites do show some hybridization.

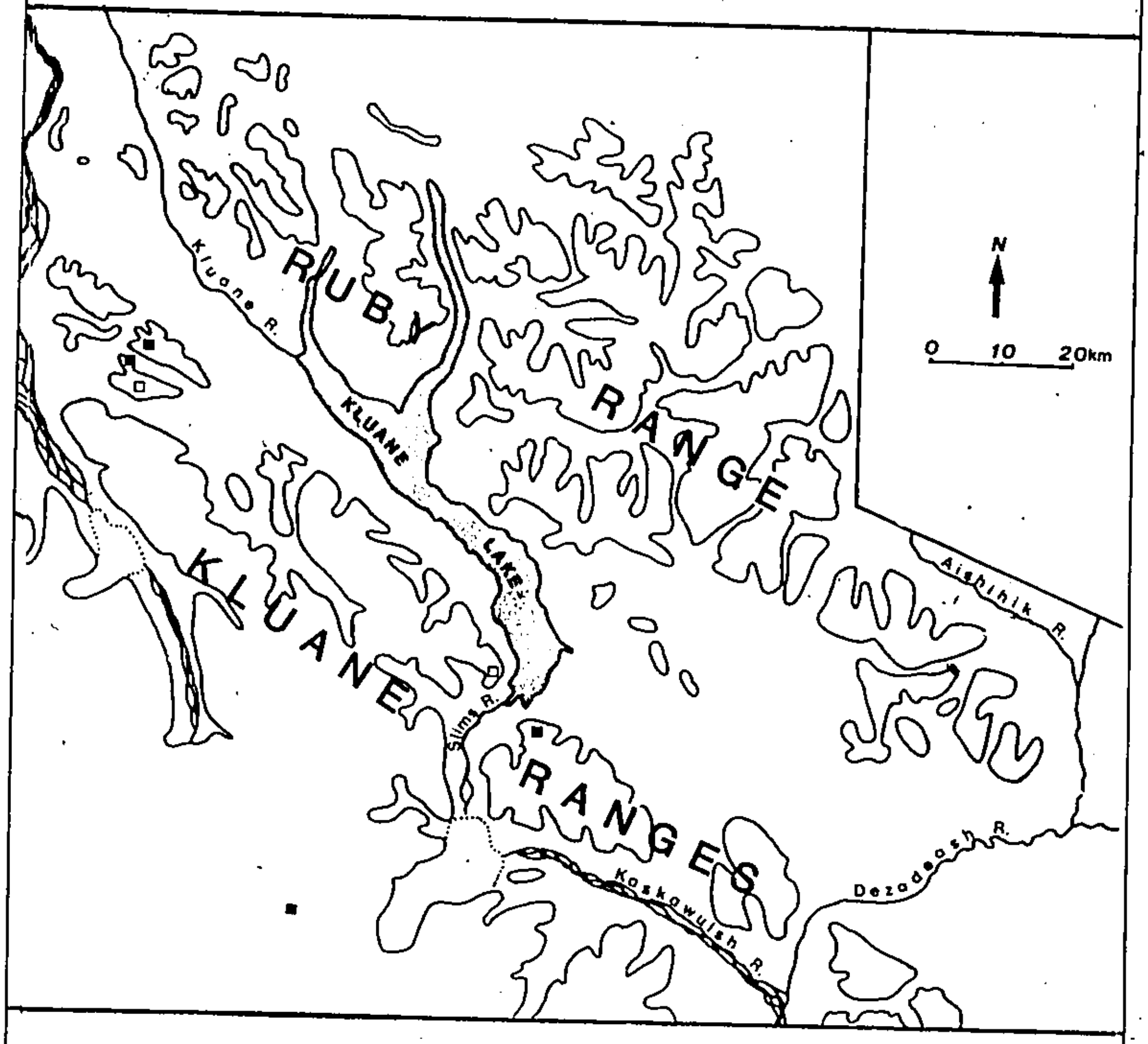


Figure 19: Occurrences of hybridization between types 2, 3 and 4. Distribution of the sampling areas where hybridization between types 2, 3 and 4 (black square) was recorded for at least one individual site, or sampling areas where all three types of hybridization have been found, but at separate sites (white square).

7.3 Ecological Analysis

7.3.1 PEGASE Models

The PEGASE program was used to explore possible explanatory models of the *Dryas* genus in the study area. A reduced version of DRYAS, RETYP (6 initial classes, further reduced to 5 by melding of a class with very low frequency to a closely related one) was the variable which described the pattern under scrutiny by PEGASE, with an initial entropy of 1.50. The chorological, climatological, geological and local environmental variables aforementioned were at first all made available to the program to find out which variables would be chosen as the major contributors of negentropy and most efficiently account for the pattern of the RETYP variable. In subsequent trials, various deletions were made to test the effects of the different categories of variables. Two major models resulted from all the trials and are described here.

With the first model which includes all categories of variables, the initial entropy was reduced by 54.2%, from 1.50 to 0.69. The variables which contribute to the negentropy are: ISLAND (31.5%), RANGE (30.7%), RELATIVE ALTITUDE (19.8%), SLOPE (9.7%) and LIME (8.3%). Note that because of the economy principle (Phipps 1981b), variables which contribute less to the negentropy can nevertheless appear before the larger contributors in the divisive pathway. Thus RANGE is the first variable chosen by PEGASE because it divides the information matrix into only two subsets, for the sharpest drop in entropy and hence most efficient division given the low number of resulting cells. The model 1 structure is as follows:

1. RANGE: Ruby Range (38 observations)
    a. LIME: Important bands of limestone. TYPES 2, 9 and 4 and 2-4 hybridization.
    b. LIME: Limestone insignificant. TYPE 2 mostly.
2. RANGE: Kluane Ranges (98 observations)

a. ISLAND: Quill Creek massif
    i. RELATIVE ALTITUDE: Lower slopes. 2-3 hybridization.
    ii. RELATIVE ALTITUDE: Intermediate slopes. Hybridization between all pure TYPES.
    iii. RELATIVE ALTITUDE: Upper slopes. Hybridization between TYPES 2, 9 and 4.
    iv. RELATIVE ALTITUDE: Summits. Predominence of TYPE 2.
b. ISLAND: Outpost massif. Hybridization between all pure TYPES.
c. ISLAND: Auriol massif. 2-3 and 2-4 hybridizations.
d. ISLAND: Kluane Lake massif
    i. SLOPES of less than 5 degrees: 2-3 hybridization.
    ii. SLOPES of 5 to 9.9 degrees: no predominence, TYPES 2, 3, 4, 9 found with hybridization.
    iii. SLOPES of 10 to 14.9 degrees: 2-3 hybridization.
e. ISLAND: Kaskawulsh. All types of hybridization.

In a second model, all chorological variables were removed. The initial entropy of 1.50 was reduced by 52% to 0.72. The contributors to negentropy are: GEOLOGY (45.1%), RELATIVE ALTITUDE (18.0%), LIME (14.0%), RAIN (12.9%) and ROCK (10.0%). Again, the economy principle was applied. LIME is the first variable chosen by PEGASE in this case, dividing the information into two subsets. The model 2 structure is as follows:

1. LIME: Important bands of limestone
    a. RAIN: 158 mm/year at closest station (Haines Junction). 2-3 hybridization.
    b. RAIN: 169 mm/year at closest station (Kluane).

- i. ROCK: Basic lava, cherty tuff, volcanic breccia, chlorite schist. All types of hybridization.
- ii. ROCK: Basalt and andesite. 2-3 hybridization mainly.
- iii. ROCK: Limestone. All types of hybridization.

c. RAIN: 182 mm/year at closest station (Burwash Landing).

- i. RELATIVE ALTITUDE: Lower slopes. 2-3 hybridization.
- ii. RELATIVE ALTITUDE: Intermediate slopes.
    - 1) GEOLOGY: chlorite schist, greenschist, quartzite, slate, quartz-mica schist, limestone (Yukon complex). Mainly TYPE 2 present, 2-9-4 hybridization, some segregated TYPE 4.
    - 2) GEOLOGY: Basic lava, cherty tuff, volcanic breccia, chlorite schist. TYPE 2 and 2-9-4 hybridization.
    - 3) GEOLOGY: Argilite, sandstone, conglomerate, limestone, chert. All types of hybridization.
    - 4) GEOLOGY: Basalt and andesite. All types of hybridization, 2-9-4 hybridization somewhat predominent.
- iii. RELATIVE ALTITUDE: Upper slopes. TYPE 2 and 9 predominent, 2-3 and 2-9-4 hybridization.
- iv. RELATIVE ALTITUDE: Summits. TYPE 2 predominent, 2-3 and 2-9-4 hybridization.

2. LIME: Limestone insignificant, if any.
    a. GEOLOGY: Quartz-biotite schist, gneiss, amphibolite (Yukon complex). TYPE 2 predominent, some TYPE 9.
    b. GEOLOGY: Granodiorite, monzonite and diorite (Ruby Range batholith). TYPE 2 exclusively.
    c. GEOLOGY: Slate, limestone, greywacke, limestone breccia, argilite, undifferentiated granitic rocks. All types of hybridization.
    d. GEOLOGY: Granodiorite and diorite (Kluane Ranges Intrusions). TYPE 3 and 2-3 hybridization.

7.3.2 Log-linear modelling

Categorical multivariate models of the log-linear type were used to corroborate the two explanatory models developed with PEGASE, and described above. Specific parts of each explanatory model which can equated to specific hypotheses about the distribution pattern as expressed by RETYP were also tested.

To approximately test the overall validity of the first PEGASE model, a log-linear model for the variables RETYP, RANGE, LIME and ISLAND was analyzed. The association of classes of those variables is very strong (Chi-square= 85.2, p= 0.0001). The testing by RANGE of LIME for the Ruby Range and ISLAND for the ~~Kluane~~ Ranges indicated strong associations, with chi-square values of 42.1 (p= 0.0001) and 57.2 (p=0.0001) respectively.

The second model was tested in much the same manner. The overall model tested included RETYP, LIME, RAIN and GEOLOGY. Association was also very strong in this case (chi-square= 71.5, p=0.001). The testing by LIME of RAIN when significant limestone is present, and that of GEOLOGY when there is not significant limestone resulted in very strong association of the variable responses (chi-square= 58.9 and 52.6, p= 0.0001 and 0.001, respectively). Both methods of multivariate categorical analysis appear to agree.

The two models developed with the PEGASE procedure adequately account for the distribution pattern, as expressed by the RETYP variable.

Chapter VIII

DISCUSSION

8.1 Typology and Taxonomy: a Comparison

The typological method based on external morphology which was adopted in this study first resulted in the identification of seven major types, of which three are clearly pure types (types 2, 3 and 4), three are intermediate types (2-3, 2-9-4, and 3-4 intermediate types), and one (type 9) has a relatively independent status, but may be not sufficiently so to give it the status of 'pure' type. The position of hybrid cluster 6 in the first factor analysis (fig. 5) and the composition of cluster 5 both appear to support the idea of an independent status, but the fact that type 2 is always present when type 9 is (figs.9 and 13) makes a clear-cut decision impossible on the basis of our regional information. However, should a taxon corresponding morphologically to type 9 have been recorded in isolation in a given region, we may then be able to confer type 9 the status of 'pure' type. Before we proceed to a comparison with taxonomical works, we will examine the results of the factor and clustering analyses for the clusters found between types 2 and 3.

Four main clusters were obtained from this second phase of the typological analysis. In spite of the rather continuous nature of the character variation (figs. 7 and 8), the clusters formed have quite distinct ranges of characteristics (table 11). Upon closer scrutiny, we find that the clusters are approximately arranged in opposed pairs: type C *versus* type D, and type A *versus* type E. Further, it appears that types C and D are extremely close to types 2 and 3 respectively, and that the more extreme specimens in each cluster should in fact be included in those respective categories. The more centrally positioned specimens of these two types probably represent the result of introgressive hybridization as discussed by Elkington (1965).

Types A , B and E all have combinations of characteristics which undoubtedly make them hybrids. Type B is only represented by two specimens which are closely related to the 2-9-4 hybridization gradient, possibly as a result of a fertile 2-3 hybrid population coming into genetic contact with a fertile population belonging to the 2-9-4 hybridization gradient. Types A and E have permutations of ~~the main~~ characteristics of types 2 and 3 which make them truly intermediate (table 11): these two types constitute the result of 2-3 hybridization.

The typology will now be compared with the taxonomical classification of Porsild, as presented in Porsild and Cody (1979) since it is the most exhaustive for North America. Porsild's classification scheme is based on the assumption that most of the stable phenotypes found have attained a level of independence in reproduction such that the taxonomic level of species is warranted (Porsild 1947).

Dryas octopetala L. is morphologically equivalent to types 2 and C: both generally have strongly crenated leaves with branched hairs only. *Dryas integrifolia* M. Vahl is related to types 3 and D: no branched hairs and very few crenations, if any. However, the extreme specimens of type 3 appear to correspond exactly to *D. sylvatica* (Hult.) Porsild. This is the result of the inclusion of the RELASIZE variable in factor 2 (table 4) which provides an additional distinction which could not be clearly isolated by the first cluster analysis. However, type D which was identified by the second clustering has average characteristics which correspond to *D. integrifolia* M. Vahl (table 11), smaller relative size included as indicated by the original position of the clusters between 2 and 3 (fig. 5).

Type 9 has been recognized by Porsild as *D. punctata* Juz. Its morphological characteristics are the presence of branched hairs —like *D. octopetala* to which it is closely related— and sessile glands (table 6). Porsild and Cody (1979) include a map of the distribution of this species showing areas in the Canadian Arctic Archipelago where only *D. punctata* has been recorded, which would indicate that this taxon has indeed reached an independent reproductive status. The morphology of *D. Hookeriana* appears to correspond to that of type 4. The crenation is coarser than that of *D. octopetala* and more importantly, there are numerous long stalked glands on the lower midvein while branched hairs are conspicuously absent (table 6). Interestingly, the type E hybrid group is conferred specific status by Porsild under the name *D. crenulata* Juz., while no mention is made of type A. In our opinion, given the constant association of types 2 and A in distribution, it does not seem justifiable to consider type A as anything more than locally segregated hybrid populations. Porsild's distribution maps actually concur at the North-American scale with our finding of a constant regional association of types 2 and E.

One last alpine species is mentioned by Porsild and Cody (1979): *D. alaskensis* Porsild. This highly variable ecotype of *D. octopetala* (McGraw and Antonovics 1983) combines the presence of branched hairs with that of stalked glands and longer leaves (Porsild 1947). It is present in wetter areas of the tundra, below or close to snowbanks (Porsild and Cody 1979, Hultén 1968). Its characteristics are such that one could expect much difficulty in differentiating between a specimen of *D. alaskensis* and a *D. Hookeriana* X *D. octopetala* specimen. In fact, while the identification must be carefully made, the stalked glands of *D. Hookeriana* are quite distinctive, being much longer, darker and purplish. Other less easily perceived characteristics also differ on average, explaining the peculiar combinations of characteristics found in type 5 which regroups hybrids between types 2, 9 and 4, as well as specimens of *D. alaskensis*. The similitude meant that an additional verification was necessary to distinguish the *D. alaskensis* specimens from the results of 2-9-4 hybridization.

The distinct advantage of having chosen the development of a typology over the use of an existing taxonomical nomenclature such as Porsild's is the additional information obtained about the nature of the relationships between the various major members of the genus in the Kluane Lake region. The use of any taxonomical scheme results in a classification which reflects the author's opinions on the taxonomy and structures the data accordingly. Furthermore, the transfer of a taxonomic classification from region to region may not be appropriate since actual regional differences may be obscured. Porsild's taxonomical nomenclature implies that each and everyone of the species mentioned above has a sufficiently independent reproductive status to justify the species level of taxonomy. In 1947, Porsild reported that hybridization between these species was not common and occurred at the local scale only.

While a parallel can be established between the typology and Porsild's taxonomy, our findings are not in general agreement with Porsild's contentions.

We do find widespread hybridization between all three main types 2, 3 and 4 (fig. 5, table 6). As for *D. punctata* (type 9), our data appear to concur with Porsild's opinion that this type can be reproductively independent, much as types 2 , 3 and 4. On the other hand, *D. alaskensis* and especially *D. crenulata* do not appear to deserve their specific status, at least not in the Kluane Lake region. While the case of D. alaskensis is quite debatable as we are dealing with an ecotype (Mc Graw and Antonovics 1983), that of *D. crenulata* is not: our data clearly show the constant geographical association of D. crenulata (type E) with *D. integrifolia* (types 3 and D) and type A, its exact opposite (no crenation but branched hairs) which Porsild does not recognize at all in his taxonomical treatment of the genus.

8.2 *Distribution Pattern and Ecology*

The striking feature of the distribution pattern is undoubtedly the total absence of *D. integrifolia* from the Ruby Range, with the possible exception of the Tincup Lake location where a single specimen of *D. crenulata* was recorded. In view of its singularity, it may well be an aberrant type, or truly represent an instance of 2-3 hybridization. Even in the Kluane Ranges, it is not the generally predominent species in the sample, with the exception of Sheep Mountain and possibly the Auriol location. In fact, it is absent from the sample of the Nickel Creek location, although its presence was recorded in all three adjacent transects.

D. Hookeriana is also restricted almost exclusively to the Kluane Ranges. But, in this case, the Tincup Lake location is a clear exception: *D. Hookeriana* hybridizes with *D. octopetala* and has also been found relatively isolated at some sites.

While *D. integrifolia* is confined to the Kluane Ranges, *D. octopetala* and the closely related ecotype *D. alaskensis* are found throughout the region, as much on soil with granodiorite as the parent material (central Ruby Range) as on soils from volcanic or metamorphic rocks, with or without limestone. *D. octopetala* has been found to hybridize with *D. integrifolia* on Sheep Mountain (fig. 14), where Hoefs et al. (1975) had recorded the latter exclusively. Even in the Kluane Ranges, *D. octopetala* and *D. alaskensis* are often the dominant species.

The distribution pattern of a given type of hybridization follows that of the parent species, as expected. Only hybrids between *D. punctata*, *D. octopetala* and *D. alaskensis* were recorded extensively in the Ruby Range. All types of hybridization occur in the Kluane Ranges because of the combined presence of several of the parent species at any given location.

8.2.1 Ecological Models

The PEGASE models identified two possible structures to account for the pattern. The first model accounts for the distribution pattern of the species at the regional level on the basis of the chorological variables RANGE and ISLAND, demonstrating the limited spatial extent of interspecific interactions, but also suggesting that species tend to occupy the alpine zone by progressive colonization of all available and suitable territory, first at the scale of the alpine island, then at the scale of the range.

One advantage of the PEGASE procedure is its ability, once the first division has been made, to seek the best descriptor for each individual class of the variable chosen at the first level. Hence, we find that in the Ruby Range, the presence or absence of limestone is chosen as the second discriminatory variable, since it accounts for the very different species composition of the Tincup Lake location. Unfortunately, it was not possible to investigate another site with limestone in the Ruby Range, which would possibly have eliminated the chorological connotation of the variable LIME for that range.

For the Kluane Ranges, PEGASE managed, despite the small size of the sample, to suggest a local altitudinal stratification. In most of the Quill Creek massif, type 3 (*D. sylvatica*) is found at the lower limit of the alpine zone and is progressively replaced by other types and their hybrids until the summits are reached, with their predominence of *D. octopetala*.

Looking at the second model in which chorological variables have been eliminated, the presence or absence of limestone (LIME) becomes the first distinguishing factor. Type 2-3 hybridization, obviously requiring the presence of type 3 (*D. integrifolia*), is most common in areas with significant limestone. However, this association does in no way imply a causal relationship. The chorological qualities of all regional variables make the identification of causal relationships extremely difficult. *D. integrifolia* and 2-3 hybrids are found in a sector of Sheep Mountain which is composed of granitic rocks but, generally speaking, the association stands.

At the second level of partitioning, RAIN is the best descriptor of the presence of significant limestone, while GEOLOGY was chosen to discriminate between those locations where limestone is absent or insignificant. Once more, at the third level of division for the presence of limestone, PEGASE identifies the altitudinal stratification of types in the Quill Creek massif with the relative altitude variable. GEOLOGY is then chosen to further subdivide the intermediate class of this particular branch, but the numbers are so low that no statistical significance can be attributed to these classes.

The question of the calcicolous or even calciphilous nature of the members of the *Dryas* genus is intriguing. Elkington (1971) does mention that it may be the relatively high combined proportion of exchangeable calcium and magnesium in the total exchange capacity which is best associated with the presence of *D. octopetala* in the British Isles. However, this appears extremely unlikely in the central Ruby Range where the parent material is granodiorite. Our results suggest that the association of calcareous parent material and presence of *Dryas* , especially *D. octopetala*, has been overemphasized. However, the PEGASE models do suggest that both *D. Hookeriana* and *D. integrifolia* may be better suited to soils with a relatively high base status, although this does not mean that a granitic parent material is excluded, as demonstrated in a sector of Sheep Mountain where *D. integrifolia* is dominant and growing on soil derived from granitic material.

The main difficulty in the interpretation of this ecological model is the problem of hidden chorology which unfortunately afflicts many of the variables. This is in part due to the lack of spatial precision of those variables (RAIN, for example), as well as to the peculiarities of their distributions. Two steps could partly alleviate this problem: further sampling, and the introduction of soil analysis variables to pinpoint edaphic parameters.

8.2.2 A Hypothetical Model of the Observed Distribution Pattern

The distribution pattern of the various types identified does not appear to lend itself to a simple ecological explanation, although the evidence is inconclusive, largely because of the nature of the variables and the distribution of their classes. It may require much more extensive sampling. However, in the event that this sampling were to be done, one might still find a large proportion of indeterminacy inherent to the measure of present environmental conditions only. After all, the structure of the *Dryas* populations has been evolving since propagules of *Dryas* first reached the region.

Endler (1983) discusses the interpretation of geographic variation and states that one must consider three elements in attempting to explain a particular distribution pattern: historical factors, current ecological factors and error. This concept can have important implications in a tentative explanation of a pattern, especially in the case of rather ubiquitous species, such as seems to be the case with *Dryas*.

Local variation can be important in the development of the pattern since population divergence can occur over distances of less than 1m (Snaydon and Davies 1976). The evolutionary divergence of adjacent populations has been extensively studied (Jain and Bradshaw 1966, McNeilly and Antonovics 1968, Snaydon and Davies 1976). From this study emerged the concept of cline (Endler 1977) or geographic gradient of variation of a phenotypic character. This concept implies a continuum of the variation in the case of widely distributed species. This type of gradient is what we find between *D. octopetala* and *D. integrifolia* in locations such as Sheep Mountain where the two species intergrade fully.

Although the species interactions are played out between populations at the microgeographic scale, the model which will be proposed here for explaining the distribution pattern will focus on the regional scale, for which most of the sampling effort was expended. While primary gene flow takes place at the scale of a few meters or at the very most tens of meters for insect-pollinated species such as those of *Dryas* (McGraw and Antonovics 1983, Faegri and Pijl 1979), the seeds, which in this case are well suited for anemochory (Pilj 1972), may be transported over considerable distances and colonize suitable habitats. As previously mentioned, the alpine zone can constitute for alpine species a habitat which is not without parallels to an archipelago. Valleys constitute barriers which, depending on their topography and physiography (rivers, lakes), and in combination with climatological conditions, can have varying degrees of porosity (Rapoport 1982). This porosity is also function of the degree of specificity of each species to the alpine habitat.

Both *D. octopetala* and *D. integrifolia* are known to be fairly aggressive invaders of open, recently disturbed habitats (Porsild 1947, Elkington 1971). We have found this to be the case at a lowland site (Christmas Bay, Kluane Lake) to which the seeds of both species have most probably been brought by water, since the site is located at the junction of two streams, one coming from the Ruby Range and the other from the Kluane Ranges. Each species has colonized a side of the stream at approximately the high water mark. Evidently, the reason for the colonization success of these two species is their competitive advantage in periodically disturbed environments such as this one. This does not appear to be a common event at low altitude since that niche is usually occupied by *D. Drummondii*.

In view of the apparently strong colonizer and invader characteristics of both species, the seemingly total absence of *D. integrifolia* from the Ruby Range is most intriguing, especially since *D. octopetala* is found throughout the Kluane Ranges. Therefore, should the Shakwak Trench be acting as a barrier to dispersal, it would be only doing so against the diffusion of a species toward the Ruby Range. Yet, *D. punctata*, which is present in the Kluane Ranges has been found at the southern boundary of the Ruby Range. However, this particular species is so closely related to *D. octopetala* that the cause of its observed distribution may be quite different. One site in the Ruby Range has shown some evidence of the possible albeit rare occurence of *D. integrifolia.* Much more common at that same location of Tincup Lake, while otherwise restricted to the Kluane Ranges is *D. Hookeriana.* A preliminary examination of wind patterns for the region seems to indicate sufficient frequency of northward winds to ensure that at least some seeds from the Kluane Ranges should eventually reach the Ruby Range.

It thus appears plausible that, in the Ruby Range at least, *D. octopetala* has a strong competitive edge over *D. integrifolia,* possibly as a result of the general nature of the substrate in the Ruby Range. This area may also be more arid than even the driest sites of the Kluane Ranges because of the rainshadow effect. Whatever the case, this competitive advantage coupled to the extremely low current availability of open sites in the Ruby Range may make successful germination and growth of a *D. integrifolia* specimen extremely unlikely. Should it manage to grow, an overwhelmingly important proportion of the gene flow being between specimens of *D. octopetala,* its genetic potential would tend to progressively be drowned out, if it continued to survive in the face of fierce competition.

But what would explain the relative success of *D. octopetala* in the Kluane Ranges? Should the Ruby Range generally have become available for colonization at a time when wind patterns favored invasion by nearby populations of *D. octopetala,* the whole of the Ruby Range might have been colonized by this single species from the beginning. Assuming that the Kluane Ranges generally became open to invasion by colonizing species at a later period, the wind patterns might have been such that a combination of species including *D. octopetala* and *D. integrifolia* might have reached the area during that colonization period. While the scenario may again include a competitive advantage for *D. octopetala,* this is by no means imperative. If *D. octopetala* is better adapted to milieus with low base status, the two species may generally be just as potentially apt to colonize open areas in most of the Kluane Ranges.

We may be witnessing the specialization of species to quite restricted niches, as appears to have happened for *D. sylvatica* which is quite probably an ecotype of *D. integrifolia*. *D. octopetala* has been found to generally occupy summit areas in the Quill Creek massif, although the result is by no means extendible to the whole of the Kluane Ranges. Similar types of specialization may be occurring elsewhere. In fact, the association of the degree of geological complexity and the number of species recorded suggests that the selective pressure toward specialization may be greater in the Kluane Ranges than in the Ruby Range.

This hypothetical model has been postulated with the goal of generating questions which may be tested experimentally and help in the explanation of the distribution pattern. It may suggest new approaches or new directions in the search for a better understanding of the nature of species distribution in space and time.

Chapter IX

CONCLUSION

The primary objective of this research was to determine the regional distribution pattern for each of the major types of *Dryas* identified in the samples from the Ruby and Kluane Ranges. This objective implied the necessity to develop an appropriate regional typology since the existing taxonomical identification schemes have serious limitations which could have created largely artificial results.

Nine types were identified in the first portion of the typological analysis, of which four have distinct characteristics and were defined in Porsild's North American taxonomical study (1947): *D. octopetala*, *D. integrifolia*, *D. punctata* and *D. Hookeriana*. One additional species was identified, this time from a cluster which also contained hybrids: *D. alaskensis* is an ecotype of *D. octopetala* which is found in wetter tundra environments. In the second phase of the typological analysis, four major types were distinguished. Two of these amount to misclassified specimens belonging to already identified clusters although, in the case of cluster D, a further distinction is made which better defines the position of *D. integrifolia* with respect to *D. sylvatica*.

All types have been found to hybridize when local demes of the various species and ecotypes are in adjacent local areas. There does not seem to be any barrier other than distance involved in the formation of hybrid populations.

While the sample size did not prove sufficiently large to provide a complete picture of local interactions for each sampling location, the PEGASE procedure did find the existence of an altitudinal stratification of types and their hybrids in the Quill Creek massif. At the base of major slopes, *D. sylvatica* is most common. It is gradually replaced by a combination of other species at intermediate levels, but forms hybrid populations with these species which occupy part of the intermediate slope environment. At the summits, *D. octopetala* takes over, although other species are found sporadically (*D. punctata, D.integrifolia* and *D. Hookeriana*).

Two models of explanation of the distribution pattern were developed with the PEGASE procedure. The first one is highly chorological: it identifies the ranges, presence or absence of limestone, and the alpine islands as those characteristics which best account for the pattern. In the second model which excludes chorological variables, presence or absence of limestone, yearly precipitation in the form of rain, and geology were chosen as those characteristics with the most explanatory power. In both cases, local variation was accounted for by the relative altitude. Finally, a hypothetical model has been developed in an attempt to generate new questions concerning the nature of the regional distribution. The most striking feature of this distribution is undoubtedly the absence of *D. integrifolia* from the Ruby Range. Because we are dealing with ubiquitous species, the ecological pattern is not clear at this point in time, even at the regional level of abstraction. The model postulated contends that the observed pattern of distribution of the *Dryas* species reflects the evolution which has taken place in the landscape since dispersal patterns and initial site conditions resulted for a given site in the exclusive establishment of a *Dryas* species or its dominance over other ones, at the time of colonization or later, through competition and resource partitioning. It is hoped that this model may serve as a tool for generating new questions and hypotheses, and hence contribute to a better understanding of the geography and ecology of *Dryas* in the Kluane Lake region.

BIBLIOGRAPHY

1. Bamberg, S.A. and Major, J., 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. *Ecol. Monogr.,* 38:127-167.

2. Barry, R.G., 1981. *Mountain Weather and Climate.,* Methuen and Co., New York, 313 pp.

3. Birks, H.J.B., 1977. Modern pollen rain and vegetation of the St. Elias Mountains, Yukon Territory. *Can. J. Bot.,* 55:2367-2382.

4. Birks, H.J.B., 1980. The present flora and vegetation of the moraines of the Klutlan Glacier, Yukon Territory, Canada: a study in plant succession *Quatern. Res.,* 14:60-86.

5. Bishop, Y.M.M., Fienberg, S.E., and Holland, P.W., 1975. *Discrete Multivariate Analysis: Theory and Practice.* The MIT Press, London, 557 pp.

6. Campbell, R.B. and Rampton, V.N., 1980. The story of the rocks and glaciers, in Theberge, J.B. (ed.), *Kluane: Pinnacle of the Yukon.* Doubleday Canada Ltd., Toronto, 175 pp.

7. Clifford, H.T. and Stephenson, W., 1975. *An Introduction to Numerical Classification.* Academic Press, London, 229 pp.

8. Cochran, W.G., 1977. *Sampling Techniques.* 3rd ed., John Wiley and Sons, Toronto, 428 pp.

9. Denton, G.H. and Stuiver, M., 1967. Late Pleistocene glacial stratigraphy and chronology, northeastern St. Elias Mountains, Yukon Territory, Canada. *Geol. Soc. America Bull.,* 78:485-510.

10. Elkington, T.T., 1965. Studies on the variation of the genus Dryas in Greenland. *Meddelelser om Gronland,* 178:1-56.

11. Elkington, T.T., 1971. Biological flora of the British Isles: Dryas octopetala. *J. Ecol.,* 59:887-905.

12. Endler, J.A., 1977. *Geographic variation, Speciation and Clines.* Princeton University Press, New Jersey, 246 pp.

13. Endler, J.A., 1983. Testing Causal Hypotheses in the Study of Geographical Variation, in Felsenstein, J. (ed.), *Numerical Taxonomy.* NATO ASI Studies, Springer-Verlag, pp. 424-443.

14. Environment Canada, Atmospheric Environment Service, 1982. *Canadian Climate Normals, 1951-1980, Temperature and Precipitation. The North: Yukon Territory and North-West Territories.* Ottawa, 55 pp.

15. Faegri, K. and Pilj, L. van der, 1979. *The Principles of Pollination Ecology.* 3rd ed., Pergamon Press, Toronto, 244 pp.

16. Forman, R.T.T. and Godron, M., 1986. *Landscape Ecology.* John Wiley and Sons, 619 pp.

17. Frontier, S., 1983. *Stratégies d'échantillonnage en écologie.* Masson et Les Presses de l'Université Laval, 429 pp.

18. Gauch, H.G., 1982. *Multivariate Analysis in Community Ecology* Cambridge University Press, New York, 299 pp.

19. Grier, C.C. and Ballard, T.M., 1981. Biomass, nutrient distribution and net production in alpine communities of the Kluane Mountains, Yukon Territory, Canada. *Can. J. Bot.,* 59:2635-2649.

20. Harman, H.H., 1976. *Modern Factor Analysis.* 3rd ed., University of Chicago Press, Chicago, 496 pp.

21. Hocking, B. and Sharplin, C.D., 1965. Flower basking by arctic insects. *Nature,* 206:215.

22. Hoefs, M., McT.Cowan, I. and Krajina, V.J., 1975. Phytosociological analysis and synthesis of Sheep Mountain, southwest Yukon Territory, Canada. *Syesis,* 8:125-228.

23. Hughes, O.L., Campbell, R.B., Muller, J.E. and Wheeler, J.O., 1969. *Glacial Limits and Flow Patterns, Yukon Territory, South of 65 Degrees North Latitude.* Geol. Surv. Canada, Paper 68-34, Ottawa, 9 pp. (1 map).

24. Hultén, E., 1959. Studies in the genus Dryas. *Svensk Bot. Tidsk.,* 53:507-542.

25. Hultén, E., 1968. *Flora of Alaska and Neighboring Territories. A Manual of the Vascular Plants.* Stanford University Press, Stanford, California, 1008 pp.

26. Jain, S.K. and Bradshaw, A.D., 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity,* 21:407-441.

27. Jessen, K., 1921. The structure and biology of Arctic flowering plants. 8. Rosaceae. *Medd. Gronland,* 37:60-74.

28. Juzepczuk, S.V., 1941. *Fl. URSS.,* Vol. 10, pp.264-279.

29. Kendrew, W.G. and Kerr, D., 1955. *The Climate of British Columbia and the Yukon Territory.* Queen's Printer, Ottawa, 222 pp.

30. Kindle, E.D., 1952. *Dezadeash Map-area, Yukon Teritory.* Geol. Surv. Canada, Memoir 268, 67 pp. (1 map).

31. Knapp, R., 1984. Perspectives on species differentiation and on hybridization in vegetation analysis and in phytosociological relevés, in Knapp, R. (ed.), *Sampling Methods and Taxon Analysis in Vegetation Science.* Dr W. Junk Pub., Boston, 370 pp.

32. Lagarec, D. and Geurts, M.A., 1984.

Les caractéristiques climatiques de la pluie pollinique dans la vallée du Gladstone Creek, Chaîne Ruby, Territoire du Yukon. Research Notes #46, Geography Dept., University of Ottawa, 33 pp.

33. Lambert, J.E., 1982. *Relative Age of Rocks Glaciers in Grizzly Creek, St. Elias Mountains , Yukon Territory, Canada.* M.Sc. Thesis, University of Guelph, 207 pp.

34. Legendre, L. and Legendre, P., 1983. *Numerical Ecology.* Elsevier Scientific Publishing Co., New York, 418 pp.

35. Leverton, D., 1981. *Vegetation, Microclimate and Soil, as Influenced by Slope and Exposure, Grizzly Creek, St. Elias Mt. Range, Yukon Territory.* M.A. Thesis, University of Ottawa, 149 pp.

36. Lunde, T., 1962. An investigation onto the pH-amplitude of some mountain plants in the country of Troms. *Acta Boreal. A. Scientia,* 20:1-103.

37. McGraw, J.B., 1985. Experimental ecology of Dryas octopetala ecotypes. III. Environmental factors and plant growth. *Arctic and Alpine Research.,* 17:229-239.

38. McGraw, J.B. & Antonovics, J., 1983. Experimental ecology of Dryas octopetala ecotypes. I. Ecotypic differentiation and life-cycle stages of selection. *J. Ecol.,* 71:879-897.

39. McKay, G.A., Findlay, B.F. and Thompson, H.A., 1970. A climatic perspective of tundra areas, in Fuller, W.A. and Kevan, P.G. (eds.), *Productivity and Conservation in Northern Circumpolar Lands.,* I.U.C.N.N.R., Switzerland, pp.10-33.

40. McNeill, J., 1984. Numerical taxonomy and biosystematics, in Grant, W.F.(ed.), *Plants Biosystematics.* Academic Press, pp.395-415.

41. McNeilly, T. and Antonovics, J., 1968. Evolution in closely adjacent populations. IV. Barriers to gene flow. *Heredity,* 23:205-218.

42. Mitchell-Olds,T. and Ruthledge, 1986. Quantitative genetics in natural populations: a review of the theory. *The American Naturalist,* 127:379-402.

43. Morris, W., (ed.), 1976. *The American Heritage Dictionary of the English Language.* Houghton Mifflin Co., Boston, 1551 pp.

44. Muller, J.E., 1967. *Kluane Lake Map-Area, Yukon Territory.* Geol. Surv. Canada, Memoir 340, Ottawa, 137 pp. (2 maps).

45. Murdock, J.R., 1951. *Alpine Plant Succession Near Mt Emmons, Uinta Mts, Utah.* M.S. thesis, Brigham Young University, Utah.

46. Naveh, Z. and Lieberman, A.S., 1984. *Landscape Ecology: Theory and Application.* Springer-Verlag, 356 pp.

47. Phipps, M. 1981a. Information theory and landscape analysis. *Proc. Int. Congr. Neth. Soc. Landscape Ecol,* 1981:57-64.

48. Phipps, M. 1981b. Entropy and community pattern analysis. *J. Theor. Biol.,* 93:253-273.

49. Pianka, E.R., 1978. *Evolutionary Ecology.* Harper and Row, Pub., New York, 397 pp.

50. Pielou, E.C., 1979. *Biogeography.* John Wiley and Sons, Toronto, 351 pp.

51. Pielou, E.C., 1984. *The Interpretation of Ecological Data: a Primer on Classification and Ordination.* John Wiley and Sons, Toronto, 263 pp.

52. Pilj van der, L., 1972. *Principles of Dispersal in Higher Plants.* 2nd ed., Springer-Verlag, New York, 162 pp.

53. Porsild, A.E., 1947. The genus Dryas in North America. *The Can. Field Nat.,* 61: 175-192.

54. Porsild, A.E., 1957. *Illustrated Flora of the Canadian Arctic Archipelago.* Bull. 146, Nat. Mus. Can., Ottawa, 209 pp.

55. Porsild, A.E., 1959. Dryas Babingtoniana, nom. nov. An overlooked species of the British Isles and western Norway. *Contributions to Botany,* Bull. 160, Nat. Mus. Can., Ottawa, pp.133-148.

56. Porsild, A.E., 1966. Contributions to the flora of southwestern Yukon Territory. *Contributions to Botany IV,* Bull. 216, Nat. Mus. Can., Ottawa, pp.1-86.

57. Porsild, A.E., 1974. *Materials for a Flora of Central Yukon Territory.* Pub. in Botany 4, Nat. Mus. Can., Ottawa, 77 pp.

58. Porsild, A.E. & Cody, W.J., 1979. *Vascular Plants of the Continental North-West Territories.* Nat. Mus. of Natural Sciences, Nat. Mus. Can., Ottawa, 667 pp.

59. Price, L.W., 1969. The collapse of solifluction lobes as a factor in vegetating blockfields. *Arctic,* 22:395-402.

60. Price, L.W., 1971. Vegetation, microtopography and depth of active layer on different exposures in subarctic alpine tundra. *Ecology,* 52:639-647.

61. Rampton, V.N., 1981. *Surficial Materials and Landforms of Kluane National Park, Yukon Territory.* Geol. Surv. Canada, Paper 79-24, Ottawa, 37 pp. (2 maps).

62. Rapoport, E.H., 1982. *Areography: Geographical Strategies of Species.* Pergamon Press, Toronto, 269 pp.

63. Reynolds, H.T., 1977. *Analysis of Nominal Data.* SAGE Publications, London, 82 pp.

64. Risser, P.G., Karr, J.R. and Forman, R.T.T., 1984. *Landscape Ecology: Directions and Approaches.* Illinois Natural History Survey Special Publication 2, 18 pp.

65. Romesburg, C.H., 1984. *Cluster Analysis for Researchers.* Lifetime Learning Publications, Belmont, CA, 334pp.

66. SAS Institute Inc., 1985. *SAS User's Guide: Statistics, Version 5 Edition.* SAS Institute Inc., Cary, NC, USA, 956 pp.

67. Snaydon, R.W., 1984. Infraspecific variation and its taxonomic implications, in Heywood, V.H. and Moore, D.M. (eds.), *Current Concepts in Plant Taxonomy.* Academic Press, pp.203-218.

68. Snaydon, R.W. and Davies, M.S., 1976. Rapid population differentiation in a mosaic environment. IV. Populations of Anthoxathum odoratum at sharp boundaries. *Heredity,* 37:9-25.

69. Sneath, P.H.A. and Sokal, R.R., 1973. *Numerical Taxonomy: the Principles and Practice of Numerical Classification.* W.H. Freeman Co., San Francisco, 500 pp.

70. Sokal,R.R., 1983. Analyzing Character variation in geographic space, in Felsenstein, J. (ed.), *Numerical Taxonomy.* NATO ASI Series, Springer-Verlag, pp.384-403.

71. Stott, P., 1984. History of biogeography, in Taylor, J.A. (ed.), *Themes in Biogeography.* Croom Helm Ltd., London, pp. 1-24.

72. Taylor, J.A. (ed.), 1984. *Themes in Biogeography.* Croom Helm Ltd., London, 404 pp.

73. Taylor, T.M.C., 1970. The Rose Family (Rosaceae) of B.C. *B.C. Prov. Mus. Pub.* 30, Victoria.

74. Taylor-Barge, B., 1969. *The Summer Climate of the St.Elias Mountain Region.* Arctic Inst. N. Amer., Res. Papp. 53, 267 pp.

75. Templeman-Kluit, D.J., 1974. *Reconnaissance Geology of Aishihik Lake, Snag and Part of Stewart Map-areas, West-central Yukon.* Geol. Surv. Canada, Paper 73-41, Ottawa, 97 pp. (3 maps).

76. Thorpe, R.S., 1983. A review of the numerical methods for recognising and analysing racial differentiation, in Felsenstein, J. (ed.), *Numerical Taxonomy.* NATO ASI Series, Springer-Verlag, pp.404-423.

77. Welsh, S.L., 1974. *Anderson's Flora of Alaska and Adjacent Parts of Canada.* Brigham Young University Press, Utah, 724 pp.

78. Wheeler, J.O., 1963. Geology, Kaskawulsh, Yukon Territory. Geological Survey of Canada, Map 1134A.

79. White, M.J.D., 1978. *Modes of Speciation.* W.H. Freeman and Co., San Francisco, 439 pp.

80. Wiggins, I.L. & Thomas, J.H., 1962. *A Flora of the Alaskan Arctic Slope.* A.I.N.A. Spec. Pub. 4, University of Toronto Press, 425 pp.

81. Willard, B.E., 1963. *Phytosociology of the Alpine Tundra of Trail Ridge, Rocky Mountain National Park, Colorado.* Ph.D. thesis, University of Colorado.