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The zonal position of *Nothofagus* forests

Die bioklimatischen Vegetationszonen der *Nothofagus*-Wälder

Las zonas de vegetación bioclimáticas de los bosques de *Nothofagus*

by

Leena HAEMET-AHTI

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1. INTRODUCTION

The genus Nothofagus is biogeographically one of the most interesting plant genera, and there are several papers dealing with its distributional history (e.g. HUMPHRIES 1981 and papers cited by him, ASH 1982). Geobotanically, Nothofagus is not less exciting, and a North European botanist is especially interested in the bioclimatic zonal position of the Nothofagus forests because they represent the southernmost forests in the world, forming the main portion of the southernmost horizontal and vertical timberlines on the globe. My purpose is to try to interpret the zonal position of the Nothofagus forests in the terms used in the northern hemisphere by my colleagues and myself (AHTI et al. 1968, HAEMET-AHTI 1965, 1976, 1979, 1981, HAEMET-AHTI et al. 1974, TUHKANEN 1980, 1984) and to accomodate this terminology to the southern hemisphere. This comparison was already started by TUHKANEN (1984), who (1980, 1984) presented the climatic indices for the boreal zone and its sectors.

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2. VEGETATION ZONES IN THE NORTHERN AND SOUTHERN HEMISPHERE

The asymmetry of the world vegetation (TROLL 1948) has had a strong influence on the concepts of vegetation geography: often the southern part of the globe is - even to-day - supposed to have fewer vegetation zones than the northern part. For instance, SCHROEDER (1983) indicates that his austral zone has three counterparts in the northern hemisphere, viz. the meridional, nemoral, and boreal zones. The concept of the austral

zone, however, seems to be too wide for many geobotanists and they have accepted more detailed concepts in their global (e.g. WALTER and BOX 1976) or local (e.g. MEURK 1984 for New Zealand) classifications. The recognition of ecogeographically corresponding units in the southern and northern amphitropical vegetation is desirable, but not easy, because of the different flora and in part the different physiognomy as emphasized, e.g. by BLISS (1979) in his comparision of arctic and antarctic vegetation. However there are some promising efforts which show that although the vegetation zones in the northern and southern hemisphere outside the tropics are not identical they are nevertheless comparable. For instance, CZAJKA's (1968) detailed descriptive profile from Alaska to Tierra del Fuego is instructive. SCHWAAR (1981) pointed out the close phytosociological relationship of some peatland communities of Tierra del Fuego with certain holarctic units, e.g. with Oxycocco-Sphagnetea. TUHKANEN (1984) even published a map on the southern counterparts of the boreal zone primarily based on the biotemperature values.

3. DISTRIBUTION OF NOTHOFAGUS FORESTS

In South America the forests dominated by the deciduous trees Nothofagus alpina. N. obliqua and sometimes N. antarctica as well as by the evergreens. N. dombeyi and N. nitida (e.g. SCHMITHUESEN 1956, OBERDORFER 1960, HUECK 1966, ESKUCHE 1968, 1969, WEINBERGER 1973, McQUEEN 1977, QUINTANILLA 1977, VEBLEN et al. 1980, HUECK and SEIBERT 1981) are obviously chiefly antitemperate but show some geographic variation due to the existence of different bioclimatic sectors or partly different subzones within the antitemperate main zone. The southern horizontal limit of the antitemperate vegetation zone lies close to 44°S (TUHKANEN 1984, p. 42) where also the southern limit of QUINTANILLA's (1977, p. 22) temperate vegetation zone also lies.

The southern counterpart of the boreal vegetation zone, the antiboreal zone, includes the deciduous forests of N. pumilio and N. antarctica, and the evergreen ones of N. betuloides (cf. the descriptions by, e.g. KALELA 1941, ROIVAINEN 1954, SCHMITHUESEN 1956, OBERDORFER 1960, HOLDGATE 1961, HUECK 1966, PISANO 1970, 1971, 1973, 1977, 1981, 1983, MOORE

1970, 1983, YOUNG 1972, ESKUCHE 1973, McQUEEN 1976, DOLLENZ 1980, 1981, 1982a, 1982b, HUECK and SEIBERT 1981). There are considerable differences in the climatic ecology between the three antiboreal Nothofagus species, as beautifully illustrated by WEINBERGER (1973) and QUINTANILLA (1977). N. antarctica and N. pumilio can be compared with the European Betula pubescens subsp. tortuosa, which forms the vertical timberline in northern Fennoscandia and is similar in physiognomy. However, N. antarctica has a wider geobotanical amplitude: its lowermost occurrences are in the antitemperate zone, often as a tree of second-growth forests. It can also form the arid timberline against the Patagonian steppes. Its uppermost limit in the mountains seems to be located in the middle oroantiboreal zone and the southernmost ones are not northern antiboreal (cf. TUHKANEN 1984). N. pumilio is mainly antiboreal; the lowermost and northernmost occurrences seem to be in the antihemiboreal subzone, and the uppermost ones in the middle antiboreal subzone.

The evergreen N. betuloides also seems to be fairly strictly antiboreal ranging up to the middle oroantiboreal subzone. The antiboreal forest vegetation in South America apparently contains the counterparts for the hemiboreal, southern boreal and middle boreal subzones only, and the middle boreal one is exclusively present as a vertical subzone. The counterparts of the northern boreal subzone do exist but are obviously completely treeless and only represented as a vertical subzone at higher elevations. The same applies to the hemiarctic subzone.

In New Zealand there are four Nothofagus species - all evergreen - forming forests and often also timberlines in mountains (e.g., P. WARDLE 1964, 1967, J. WARDLE 1970, GODLEY 1975). In fact, the ranges of N. truncata and N. fusca are apparently antimeridional to (oro) antitemperate, while N. menziesii and N. solandri are mainly antitemperate to oroantiboreal. According to MEURK's (1984) terminology the range of the first two species is warm to cool temperate and that of the last two species temperate to subantarctic. The antiboreal zone occurs on the South Island of New Zealand only vertically on the slopes of the mountains. The upper oroantiboreal subzone seems to be completely treeless, because the horizontal timberline formed by Nothofagus is located in the middle of the lower oroantiboreal subzone or sometimes even down in it. If we compare the climatic values of the timberline areas in New Zealand (e.g. MORRIS 1965) with parameters published by TUHKANEN (1984) for the boreal zone they indicate highly oceanic middle boreal climate with a

cool but long growing period. This is also distinctly seen in P. WARDLE's (1965, 1971, 1972, 1977) comparisons of the New Zealand timberlines with some North American and Eurasian ones. His experiments to grow some North American timberline trees above the tree line in New Zealand are very inspiring (cf. P. WARDLE 1971, 1972, 1973), but again distinctly show that the timberline is not always an equivalent line in the different mountains (cf. HAEMET-AHTI 1979). The timberlines in New Zealand also differ physiognomically from most of the timberlines in southern South America because all the timberline trees, including the Nothofagus species, in New Zealand are evergreen rather than deciduous.

In Tasmania there is the only deciduous Nothofagus species of the eastern hemisphere, viz. N. gunnii. It forms stands on exposed sites in high mountains, sometimes close to the timberline (e.g. JACKSON 1965, HOWARD 1981, COSTIN 1981, MINCHIN 1981). N. gunnii seems to occur in the oroantitemperate and perhaps also oroantihemiboreal zone. In SE Australia there are two Nothofagus species: N. gunninghamii, which also occurs in Tasmania, and N. moorei (e.g. HOWARD and HOPE 1970, HOWARD 1973, 1981, HOWARD and ASHTON 1973). They are evergreen and apparently antimeridional to antitemperate.

In New Guinea several species of the genus Nothofagus which all are evergreen occur (ASH 1982). The occur in the lower, middle, and upper montane zone, being frequent only in the middle montane zone (JOHNS 1982). The zones apparently correspond to the horizontal subtropical, meridional, and southern temperate (= northern antitemperate) zones. In New Caledonia there are also many Nothofagus species and geobotanically they seem to be much like the New Guinean ones (cf., DAWSON 1966, VAN STEENIS 1971). In New Guinea as well as in New Caledonia Nothofagus is not a timberline tree and is most abundant in the oroantimeridional zone, far below the timberline (e.g. ASH 1982).

If we compare the northernmost and southernmost timberline forests of the globe, the roles of the needle-leaved and broad-leaved, as well as the evergreen and deciduous, tree species seem to be different on the different continents contrary to some customary generalizations.

4. COMPARISON OF THE NOTHOFAGUS FORESTS TO EURASIAN FORESTS

At the horizontal and vertical timberlines in northern Eurasia there are deciduous broad-leaved trees (Betula pubescens subsp. tortuosa, B. ermanii, Alnus maximowiczii) in the most oceanic areas (HAEMET-AHTI and AHTI 1969) and the deciduous needle-leaved conifers (Larix sibirica, L. gmelinii) in the most continental areas. Amongst these the evergreen conifers (mainly Picea abies subsp. obovata) predominate. In North America deciduous broad-leaved trees (Alnus sinuata) occur at the timberline only in southeastern Alaska and adjacent Canada. The whole truly polar timberline is formed by evergreen conifers (Picea glauca, P. mariana and in the easternmost part Abies balsamea), and among them a deciduous conifer (Larix laricina) is common, especially in the continental areas (e.g. HUSTICH 1966). In the southernmost part of the southern hemisphere there are no conifers at the timberline. The evergreen broad-leaved trees (N. betuloides) occur in the extremely oceanic part of southernmost South America as well as in New Zealand (N. menziesii, N. solandri). The deciduous broad-leaved trees (N. pumilio, N. antarctica) occur at the timberline in southernmost South America only.

Also the forests at the margins of the steppe areas under boreal and antiboreal circumstances are quite different in the different continents. In Eurasia boreal steppes or steppe patches are surrounded by deciduous conifers (e.g. Larix gmelinii in northern boreal Yakutia, L. sibirica in hemiboreal northern Mongolia), and in North America either by evergreen conifers (Picea glauca in the northern and middle boreal Yukon) or by deciduous broad-leaved trees (Populus tremuloides and P. balsamifera in the hemiboreal part of Alberta). In South America deciduous broad-leaved trees (Nothofagus antarctica) occur on the margins of the southern Patagonian antihemiboreal and northern antiboreal steppes.

There is hardly any general rule to explain the occurrence of these taxonomically, ecomorphologically, and physiognomically different tree species at the northernmost or southernmost timberlines. These timberlines are geobotanically simply not identical, and they are caused by different minimum factors (e.g. excessive cold, aridity, humidity, wind, or their combinations). It seems unlikely that we should be able to find a general law based only on the present climatic or other ecological circumstances. For instance, the concept of the diurnal climate (TROLL

1948 etc.) as a reason for the lack of the deciduous Nothofagus species in New Zealand was shown to be untenable by P. WARDLE (1963), who found growth rings and other indications produced by a distinctly seasonal climate there.

It is also necessary to consider the history of the flora when we make large-scale geobotanical comparisons over the globe, as stated by many authors in different connections (e.g. by DU RIETZ 1960, HUEBL 1969, HAEMET-AHTI and AHTI 1969, WALTER 1977, HAEMET-AHTI 1978, KLOETZLI 1983). The individual migrational histories of each species are expected to provide a logical explanation for the diversity in the present-day ranges and ecology of the Nothofagus species.

SUMMARY

The bioclimatic vegetation zones of the Nothofagus forests in southern South America and New Zealand are antitemperate to middle (oro) antiboreal, in Australia antimeridional to antitemperate, in New Guinea and New Caledonia subtropical to antitemperate. Nothofagus species are timberline trees only in South America and New Zealand, and geobotanically the highest Nothofagus timberlines in both areas are obviously in the middle oroantiboreal subzone. In South America there are deciduous and evergreen species at the timberline, while in New Zealand only evergreen species are present. There is hardly any general rule based on the present ecoclimatic conditions to explain the occurrence of the evergreen versus deciduous broad-leaved or evergreen versus deciduous coniferous tree species at different kinds of timberlines in the northernmost and southernmost parts of the globe. The main reason for the present distribution of the different ecophysiognomic elements is apparently the history of the flora.

ZUSAMMENFASSUNG

Die bioklimatischen Vegetationszonen der Nothofagus-Wälder in Südamerika und Neuseeland sind antitemperiert zu mittel(oro)antiboreal, in Australien antimeridional zu antitemperiert, in Neu-Guinea und Neukaledonien subtropisch zu antitemperiert. Nothofagus-Arten bilden Waldgrenzen nur in Südamerika und Neuseeland. Die höchste Waldgrenze in den beiden Gebieten ist wahrscheinlich in der mittel-oroantiborealen Zone. In Südamerika gibt es sommergrüne und immergrüne Arten an den Waldgrenzen während in Neuseeland nur immergrüne Arten vorkommen. Es gibt kaum eine allgemeine Regel, die aufgrund der heutigen ökoklimatischen Verhältnisse das Vorkommen der immergrünen und sommergrünen Laubbäume oder der immergrünen und sommergrünen Nadelbäume an den verschiedenen Waldgrenzen in den nördlichsten und südlichsten Teilen der Erdkugel erklären könnte. Der Hauptgrund der heutigen Vorkommen der verschiedenen ökophysiognomischen Elemente ist wahrscheinlich die Geschichte der Flora.

RESUMEN

Las zonas de vegetación bioclimáticas de los bosques de Nothofagus en Sudamérica y Nueva Zelandia son antitemperadas a medio-(oro)antiboreales; en Australia son antimeridionales a antitemperadas. Solamente en Sudamerica y en Nueva Zelandia, especies de Nothofagus establecen límites de bosque. En las dos regiones, el límite de bosque mas elevado se encuentra, probablemente en la zona medio-oroantiboreal. En Sudamérica hay especies caducifolias y siempreverdes en los límites de bosque, solamente siempreverdes en Nueva Zelandia. Acaso existe una regla general para explicar la presencia de los arboles caducifolios o siempreverdes, sean latifoliados o acicularifolios, en los diferentes límites de bosques en los extremos boreales y australes del globo terrestre bajo las condiciones del clima actual. La distribución actual de los distintos elementos ecofisionómicos se debe, probablemente, a la historia de la flora.

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