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A tree of many faces: Why are there different crown types in Norway spruce (*Picea abies* [L.] Karst.)?

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The authors would like to dedicate this paper to Professor Dr. Peter Schütt on occasion of his 80th birthday

Abstract

Norway spruce (*Picea abies* [L.] Karst.) has a pronounced ability to create different crown types embracing strongly hypotonic, epi-hypotonic, strongly amphitonic types as well as respective intermediate ones. Data of Holzer and Schultze (1987) were reanalyzed in order to identify major environmental components that may shape ecotypes and contribute to Gruber's (1989) hypothesis that phenotypic plasticity is different among different crown types. Environmental variables and crown types were assessed by Principal Components Analysis. The first principal component explained 74% of the variation that was mainly loaded by different temperature variables and altitude while the second principal component explained additional 23% mainly loaded by precipitation variables. Orientation had a statistically significant but small effect. Covariance analysis demonstrated that age had modified crown type in a way that more hypotonic types were phenotypically more variable. Overlaps between crown-type distributions were evaluated by Schoener's Index, which may range from 'zero' (no ecotypic overlap) to 'one' (complete ecotypic overlap). In the present paper this index resulted in pairwise values varying from 0.21 to 0.86. The ecotypic overlap matrix was symmetric, i.e. ecotypic pairs increased gradually with stepwise crown-type graduation. We discussed the adaptation strategy of Norway spruce based on our results and propose that adaptation in this species regarding crown architecture is mainly caused by adaptive differentiation in higher altitudes while in lower elevations phenotypic plasticity is the dominating factor.

Keywords: Adaptability; Adaptive differentiation; Crown types; Ecotype; Schoener's Index; Phenotypic plasticity

Introduction

Above-ground architecture of trees is a question of cost–benefit relationship (Küppers, 1989), evolutionary requirements both for vegetative (Smith and Brewer, 1994) and reproductive survival of the species. Thus, crown architecture is related to the central problem of the ability of a tree (species) to survive in a competitive environment.

As long as a tree gains more carbon than it requires for its crown development and evolutionary needs it will survive. Crown development has been predicted by several allometric equations (e.g., Ilomäki et al., 2004; Kantola and Mäkelä, 2004). However, to understand

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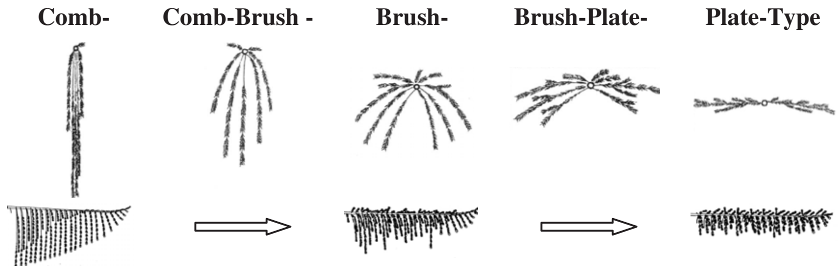

Fig. 1. Phenotypes in *Picea abies* according to second-order orientation of branches (Gruber, 1989, modified).

the ecological significance of tree crowns it is necessary to take an integrated view of morphological, architectural, physiological and genetic attributes in concert (Tomlinson, 1983).

Crowns of different tree species vary considerably and are often species specific. Surprisingly, Norway spruce (*Picea abies* [L.] Karst.) forms different crown types. Like most other woody species it has a metameric crown architecture, i.e. certain units of morphogenesis are periodically repeated resulting into a characteristic genetically determined repetitive branching pattern. But the second-order branching pattern may vary strongly leading to very different crown types in this species that was firstly described by Sylvén (1909). He differentiated among strongly hypotonic (so-called comb type) through epi-hypotonic (so-called brush type) to strongly amphitonic (so-called plate type) crowns. This architectural pattern was later confirmed by many other authors (e.g., Alexandrov, 1971; Holzer, 1964; Priehäusser, 1958; Schmidt-Vogt, 1972a). Crown types were considered stable over time; however, Schmidt-Vogt (1972a) assumed that certain types would be more stable than others. Gruber (1988, 1989) confirmed this thought by studying several ramets in a Norway spruce seed orchard in comparison to the forms of the respective ortets and proposed three genetically determined crown types (genotypes) that would differ in their reaction norms resulting into different phenotypic plasticities. At least five crown forms could be differentiated.

The objective of this study was to investigate (1) how crown types of *P. abies* are related to different environmental data within the species' natural range in Austria and (2) finally, we link our results to Gruber's (1989) hypothesis of differing phenotypic plasticities and discuss adaptation strategies for this tree species.

Material and methods

Study area and sampling

Data were collected within the framework of the National Forest Inventory (NFI) conducted throughout Austria in 1981/85 on a regular grid system of $3.89 \times 3.89\,\mathrm{km}^2$. These data on crown types of Norway spruce were previously published by Holzer and Schultze (1987) and were reanalyzed in the present study. Each grid point of the regular grid system consisted of a square with a side length of 200 m. The vertices of this square were in the center of circular plots ($300\,\mathrm{m}^2$) in which all trees were scored. From the original data, (1) entries of artificial plantings of allochthonous populations according to Prskawetz and Schadauer (2000), (2) trees that could not be scored properly in the field (see *Assessment of crown type*) and (3) trees exceeding a certain age (see *Assessment of tree age*) were excluded. The reduced data set consisted of 12,921 trees.

Assessment of crown type

In each plot, different crown types of Norway spruce were visually assessed and characterized according to Fig. 1 into five types: (1) strongly hypotonic comb type [C-type], (2) comb-brush type [CB-type], (3) epi-hypotonic brush type [B-type], (4) brush-plate type [BP-type] and (5) strongly amphitonic plate type [P-type]. For 1255 trees (approximately 8% of the initial data) the individual crown type could not be assessed reliably in the field, for instance due to damages on branches and foliage. These data were excluded from the analysis. Cohorts of the five crown types were regarded as 'ecotypes',[1] although the knowledge of the genetic basis of plastic crown reaction is scarce.

Assessment of tree age

The parameter 'age of a tree' was assessed in the field along an ordinal scale distinguishing seven classes: $\leqslant 20$, 21–40 …, 121–140 years. The age was estimated by counting annual rings of stumps or wooden drill cores.

[1]The term 'ecotype' is used in this paper in its most general meaning. Whenever ecotypic variation or its significance has not been fully understood, Gregor (1944) has suggested the term 'ecodeme' instead. However, this term is very seldom used and may not be well known among many of the readers.