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Investigations on the Correlation Pattern in Even-Aged Stands of Larch

II. Dynamic Description of Phenotypic Correlations Between Neighbouring Observations[1])

By M. HÜHN[2]) and W. LANGNER[3])

Summary

The main topics of this study are a dynamic description of spatial neighbourhood correlation patterns of stands of larch and an analysis of temporal changes and time trends of such patterns during stand development. For these investigations extensive data sets from a field trial with 27 "entries" (5 *Larix europaea*, 15 *Larix leptolepis*, 7 hybrids) have been used. Single tree measurements of this trial were available for 7 stages of stand development (ages: 11, 13, 18, 19, 42, 49 and 50 years). The measured traits are height and diameter at breast height. For the 2 ages 42 and 49 only diameter measurements were available. Additionally, the diameter values are transformed and analysed as individual basal areas.

The correlative structure of this trial for measurements of neighbouring individuals [regular square spacing with wide spacings (5 m x 5 m), no artificial thinning procedures] has been described by 12 different correlation coefficients. These coefficients are defined by considering quite different spatial configurations of competitive neighbourhoods. In these procedures and analyses the diagonally located neighbours of a subject tree and its missing neighbours too are explicitly considered.

For the trait height one obtains for all ages a quite uniform correlation pattern: positive correlations with intermediate numerical amount between the trait measurement of a subject tree and the corresponding value of its neighbourhood (for different spatial definitions of neighbourhood) and less stronger negative correlations between the trait measurement

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of a subject tree and the number of missing neighbours in its neighbourhood.

The correlation patterns for the traits height and diameter are coincident for the "early" period of stand development (11 to 19 years). This coincidence is true for the sign as well as for the approximate numerical amount of the different correlation coefficients. For the "late" period of stand development (50 years), however, one obtains substantial differences between the correlation patterns for height and diameter. The correlations between the diameter measurement of a subject tree and the corresponding value for the sum of its neighbourhood are negative (for height they are positive) and the correlations between the diameter measurement of a subject tree and the number of missing neighbours in its neighbourhood are positive (for height they are negative).

In this wide spacing trial the correlation coefficient between height and diameter strongly decreases from 0.88 at age 11 up to a surprisingly small value of 0.34 at age 50, i.e. the relationship between height and diameter disappears during stand development.

The estimates of the correlation coefficients as well as their detected interrelationships are of high reliability since the correlation calculations of this study are based on very large numbers of observations (smallest sample size = 1081, largest sample size = 6279).

Zusammenfassung

Für die dynamische Betrachtung des räumlichen Korrelationsmusters von Lärchenbeständen, d. h. für die Analyse der Nachbarschaftskorrelationen eines Bestandes zu unterschiedlichen Zeitpunkten seiner Entwicklung sowie für eine Diskussion der zeitlichen Veränderung dieses Korrelationsmusters, wurde eine Versuchsfläche mit 27 „Sorten" (5 Europalärchen, 15 Japanlärchen, 7 Hybriden) ausgewählt, die zu 7 verschiedenen Zeitpunkten der Bestandesentwicklung (Alter: 11, 13, 18, 19, 42, 49 und 50) einzelbaumweise vermessen wurde. Die erhobenen Merkmale sind „Höhe" und „Durchmesser". Für die beiden Alter 42 und 49 stand nur eine Durchmessermessung zur Verfügung. Zusätzlich werden die Durchmesserwerte transformiert und als individuelle Grundflächen ausgewertet.

Die Nachbarschaft-Korrelationsstruktur des im sehr weiten quadratischen Verband (5 m x 5 m) angelegten und auch nicht-durchforsteten Lärchenbestandes wird durch 12 verschiedene Korrelationskoeffizienten beschrieben, die durch die Heranziehung von unterschiedlichen räumlichen Nachbarschaftskonfigurationen definiert werden. Dabei werden auch diagonal entfernt stehende Nachbarn sowie auch fehlende Nachbarn explizit in die Ansätze und Auswertungen mit einbezogen.

Für das Merkmal „Höhe" erhält man für sämtliche Alter ein sehr übereinstimmendes Korrelationsmuster: positive Korrelationen mittlerer numerischer Höhe zwischen dem Merkmalswert eines Baumes und dem entsprechenden Wert für seine Nachbarschaft (bei unterschiedlichen räumlichen Definitionen von Nachbarschaft) und wenig straffe negative Korrelationen zwischen dem Merkmalswert eines Baumes und der Anzahl Fehlstellen in seiner Nachbarschaft.

Für die „frühe" Entwicklungsphase des Bestandes (11 bis 19jährig) stimmt das Korrelationsmuster für das Merkmal Durchmesser mit dem für das Merkmal Höhe überein – und zwar sowohl im Vorzeichen als auch näherungsweise in der numerischen Höhe der verschiedenen Korrelationskoeffizienten. Für die „späte" Entwicklungsphase (50jährig) zeigt sich jedoch ein überaus deutlicher Unterschied: Die Korrelationen zwischen dem Durchmesserwert eines Baumes und dem entsprechenden Wert für die Summe seiner Nachbarschaft sind negativ (für die Höhe waren sie positiv) und die Korrelationen zwischen dem Durchmesserwert eines Baumes und der Anzahl Fehlstellen in seiner Nachbarschaft sind positiv (für die Höhe waren sie negativ).

In diesem Versuch mit sehr weitem Standraum fällt die Korrelation zwischen Höhe und Durchmesser von 0,88 im Alter 11 auf 0,34 im Alter 50 sehr stark ab, d. h. die Beziehung zwischen Höhe und Durchmesser geht im Verlauf der Bestandesentwicklung praktisch verloren.

Den geschätzten Korrelationskoeffizienten sowie den zwischen ihnen aufgefundenen Größenbeziehungen kommt eine hohe Zuverlässigkeit zu, da diese Korrelationsberechnungen auf sehr großen Anzahlen von Beobachtungswerten beruhen (kleinster Stichprobenumfang = 1081, größter Stichprobenumfang = 6279).

Introduction

For many applications in the fields of forest genetics and forest tree improvement and, of course, for silvicultural practices too, an insight into the spatial correlation patterns of the underlying populations is of particular relevance. Two examples are 1) the estimation of competitional components of the phenotypic variance based on the correlations between the measurements of neighbouring individuals and 2) utilization of spatial neighbourhood correlations for certain selection procedures to increase the selection response.

Phenotypic correlations between height measurements for neighbouring individuals have been reported and studied by KENNEL (1966), STERN (1966), SAKAI et al. (1966, 1968), SAKAI and MUKAIDE (1967) and STERN (1968a). Many of these phenotypic correlations were negative, i. e. smaller individuals were often adjacent to taller ones and vice versa.

Studies of patterns of spatial correlations are, of course, closely related to an analysis of competitive effects. Many competition indices and measures of stand density have been developed and used in the fields of forest mensuration and forest inventory in predicting growth of trees and stands. "Most competition indices are considered to be a measure of the degree to which growth resources may be limited by the number, size, and proximity of neighbours. The resources involved and their absolute availability may not be well defined, but may include, at least conceptually, light, water, nutrients, and physical growing space. Other competition measures have been developed that attempt to quantify the relative availability of resources. Point density measures are an attempt to quantify the density affecting a given point (or tree) in a stand. These measures may be thought of as competition indices that express a tree's competitive status in terms usually associated with stand level density measures, such as trees or basal area per hectare.

The biological processes involved in competition among trees are much more complex than can be described by a single mathematical index. However, such indices do provide measures of the outcome of these processes and they have been found useful in predicting tree growth" (DANIELS et al., 1986).

The most simple class of competition indices is based on circular areas of influence for each individual tree where the area may be a function of the tree size. The competitive stress is measured as the degree of overlap between the influence area of an individual tree and those of its neighbours (BENJAMIN and HARDWICK, 1986; DANIELS et al., 1986). The density at each tree can be defined in terms of the numbers of circles including the tree.

For irregular spatial patterns of the individual trees of a stand an useful competition index has been introduced by

BROWN (1965): Polygons are constructed around the subject tree by bisecting intertree distances between the subject tree and its competitors. Polygon area is calculated from the coordinates of the polygon vertices. The polygon area is the area potentially available for tree growth. This measure partitions the total stand area and the associated resources into those parts which are potentially available for each individual tree. These so-called Thiessen-polygons or Voronoi-polygons are, of course, mutually exclusive and collectively exhaustive of the total area.

A discussion and comparison of different competition indices has been published by OPIE (1968), DANIELS (1976), NOONE and BELL (1980), MARTIN and EK (1984), DANIELS et al. (1986) and BIGING and DOBBERTIN (1992). Numerous modifications and generalizations have been worked out. In general, the results of these comparisons have been quite variable. The performance of a particular index may vary with species, stage of stand development and cultural practices. No index has been shown to be universally superior.

But, the common idea of all these concepts is the assumption that the areas exploited by each tree can be represented by a set of "zones of influence" which may be defined by purely spatial considerations. Each "zone of influence" can be assigned a quantitative measure, its "space", where the amount of this "space" reflects the availability of environmental factors. Various definitions of "space" have been used (MEAD, 1979; BENJAMIN and HARDWICK, 1986). The basic idea for all these quite different approaches is the assumption that the trait value of a tree can be considered as a function of "space" per tree.

Much attention has been paid to the analysis of differences between trees generated by the disproportionate sharing of resources within the stand caused by different available "spaces". By these considerations we may expect, that the variability of all individual measurements of a certain trait in the population and its inherent spatial patterns will be approximately reflected by homologous patterns of the corresponding competition indices, zones of influence, and spaces, respectively.

Actual developments in silvicultural yield and growth research deal with a transition from the traditional volume growth-oriented yield science (static approaches based on the sums or means of the stands) to a system-oriented science of forest growth (dynamic approaches based on single stems, i. e. decomposition of the stand into a mosaic of individual trees and modelling of stand development as a dynamic space-time system). Such a description of the development of the single stems of a stand in dependence of locational conditions and spatial growth constellations requires a comprehensive knowledge and handling of competition indices which appropriately reflect the actual growing conditions for individual stems in stands with nonregular spatial patterns (PRETZSCH, 1995).

To get some deeper insight into these complex relationships, correlation analysis of spatial patterns of observed values may provide an useful approach.

Problem

Measures of spatial similarity have been obtained through correlation analyses by many authors where the correlation coefficients are computed in the usual manner for neighbouring observations. In addition to the references cited in Section 1 (Introduction) some further relevant publications are CANNELL et al. (1984), TUSKAN and MC KINLEY (1984), GILLESPIE and HOCKER JR. (1986), MAGNUSSEN (1990, 1994) and BIGING and

DOBBERTIN (1995) and the highly recommendable textbooks of CLIFF and ORD (1981) and RIPLEY (1981).

A widely used attempt to assess the extent of spatial correlations is the computation of correlation coefficients for first-, second-, and third-order neighbours. The order of the relationship refers to the spatial closeness of the observations. First order neighbours share common borders, second-order neighbours have common first-order neighbours etc.

In the present study, 4 main topics from the analysis of spatial correlation patterns of even-aged populations of larch will be investigated:

No. 1. Pattern analysis by phenotypic correlations between neighbouring observations for quite different spatial configurations of neighbourhoods. In this context diagonal trees are also considered as neighbours.

No. 2. Evaluation and comparison of the spatial correlation pattern results for the traits height, diameter at breast height and individual basal area.

No. 3. In practical forestry, plantations for production purposes are commonly established with regular planting patterns (for example, regular square spacing or regular row spacing). But, during stand development nonregular patterns necessarily arise by effects of natural mortality, thinning treatments etc. What are the effects of missing trees on the resulting spatial correlation pattern?

This topic No. 3 involves a consideration of temporal changes of the plantation's planting configuration and its spatial neighbourhood pattern. This point of view leads to the central question of this study: Description and analysis of tree growth and stand development by incorporating dynamic measures and models of tree interferences and plant community dynamic processes.

Most indices of tree competition are based on various measurements of the abundance, proximity, and stature of neighbouring trees, which are usually measured at only one point in time, i. e. these competition indices are static! They are based on a single set of measurements without any explicit consideration of the many sources of variation within a stand and from year to year. But, "system dynamics cannot be represented by one-time measurements. Perhaps the most important limitation of any competition index is that it is static; it is a representation of the state of a dynamic system at one point in time. Instantaneous assessments cannot unequivocally determine the importance of interference" (BURTON, 1993).

In the framework of non-static descriptions, trends in variances and covariances dependent on age have been reported by many authors (NAMKOONG et al., 1972; NAMKOONG and CONKLE, 1976; FRANKLIN, 1979; LAMBETH, 1983; LAMBETH et al., 1983; KANG, 1985; FOSTER, 1986; GILL, 1987; HÜHN et al., 1987; RIEMENSCHNEIDER, 1988; BENTZER et al., 1989; BURDON, 1989; HÜHN and KLEINSCHMIT, 1989 and 1993; OTEGBEYE, 1991; JINDAL et al., 1992; BALOCCHI et al., 1993; MATHESON et al., 1994; SATO, 1994). A knowledge of such temporal changes and time trends of essential parameters (for example, heritability) is of particular importance for many problems and decisions in forest tree improvement programs (optimum selection age, appropriate traits, choice of selection methods etc.).

Closely related to these investigations are the innumerable studies on age-age correlations to utilize such juvenile-mature correlations for early selection purposes. In this context, however, we don't enter into a discussion of this topic.

Since the mutual competitive effects between neighbouring individuals are different in different ages or in different stages of stand development, the spatial correlation patterns too must be dependent on time.

An interesting attempt to incorporate such a dynamic point of view into an analysis of spatial neighbourhood correlations has been carried out by STERN (1968b). He calculated multiple phenotypic correlations between the measurement of a subject tree and the measurements of its competitive neighbours including their measurements in several preceding ages. The resulting multiple correlation coefficients were considerably larger than the simple correlations.

In the present study, all investigations on spatial neighbourhood correlation patterns are restricted to only one field trial and we are interested in a dynamic description. The fourth main topic of this paper, therefore, can be summarized as: No. 4. Dynamic description and analysis of temporal changes and time trends of the neighbourhood correlation pattern during stand development.

In this study, some empirically-based contributions to No. 1 to 4 will be presented without intending any comprehensive discussion of the underlying phenomena.

Material and Methods

This study is based on extensive data sets of single tree measurements for height and diameter at breast height for one even-aged larch population, which had been measured at 7 different stages of stand development (from age 11 up to age 50). The plant material of this field trial consists of 27 entries which belong to 3 groups of different origin (*Larix europaea*, *Larix leptolepis*, and their hybrids). These 27 entries (5 *Larix europaea*, 15 *Larix leptolepis*, 7 hybrids) have been tested at the site "Gahrenberg" near Göttingen/Germany (degree of longitude 9°36'; degree of latitude 51°28') (area ≅ 6 ha). This Gahrenberg-trial is the oldest experiment in Europe to examine the performance of hybrids relative to their parents (initial crosses in 1936, establishment of the plantation in spring 1939 with 2 years old plants). A detailed description of all interesting aspects (parental material for the crosses, performance of the crosses, nursery practices, characteristics of the site, information on the establishment of the plantation, design, replications, plot size, handling of the measurements etc.) was published by LANGNER (1951, 1952) and we refer to these 2 publications.

This field trial was established as a regular square spacing (5 m x 5 m). These wide plant spacings ensured a delayed beginning of the competitive pressure among neighbouring trees. Competition starts at an stage of stand development when all the competitive interrelationships between crop trees and the noncrop vegetation are eliminated. By this approach a confounding of competitive effects between neighbouring crop trees and competitive effects between crop trees and noncrop vegetation can be avoided. The calculated spatial correlations for this wide-spacing-trial, therefore, reflect the "true" neighbourhood pattern between competing trees unaffected by other competitive interrelationships.

Some further characteristics with special relevance for this study have been compiled in *table 1*. No systematic artificial thinning procedure has been applied. But, nevertheless, a moderate reduction of the number of living trees (= population sizes from *table 1*) was observed. These reductions of approximately 11% from age 11 up to age 50 are caused by natural mortality and other unevitable events (*Tab. 1*).

Comparisons of the results of this Gahrenberg-trial with results obtained from traditional silvicultural experiments must be carried out cautiously since the latter are usually established with much closer plant spacings (see, for example: RÖHRIG, 1995).

Table 1. – Some characteristics of the field trial (Gahrenberg) used in this study.

Measure-ment No.	Measured traits height	Measured traits diameter	Measurement at age (in years) height	Measurement at age (in years) diameter	Population size height	Population size diameter
1	yes	yes	11	11	1342	1342
2	yes	yes	13	13	1323	1323
3	yes	yes	18	18	1292	1292
4	yes	yes	19	19	1249	1249
5	no	yes	-	42	-	1208
6	no	yes	-	49	-	1198
7	yes	yes	50	50	1197	1197

In this study we are interested in spatial neighbourhood correlation patterns. To exclude all irregular neighbourhood configurations, all border trees of the plantation were dropped from the analyses. Thus, only observations with a complete array of neighbours were included in these analyses. These potential neighbours, however, may be still living or already missing at the time of measurement.

Based on single tree measurements, simple product moment or PEARSON correlation coefficients were calculated between each single tree measurement and several measures which are based on individual tree measurements of the competing neighbours of the subject tree. These different measures are defined by the consideration of quite different spatial configurations of neighbours which are assumed to be effectively competing neighbours of the subject tree. Particular emphasis is given to the fact that missing values will affect the resulting spatial correlation pattern substantially.

The spatial correlation patterns are described by the following correlation coefficients (*Figure 1*):

r_1 = correlation between subject tree X and sum of its direct neighbours D, B, E, and G, respectively.

r_2 = correlation between subject tree X and sum of its diagonal neighbours A, C, H, and F, respectively.

r_3 = correlation between subject tree X and sum of its direct and diagonal neighbours.

r_4 = correlation between subject tree X and mean of its direct neighbours.

r_5 = correlation between subject tree X and mean of its diagonal neighbours.

r_6 = correlation between subject tree X and mean of its direct and diagonal neighbours.

r_7 = correlation between subject tree X and 1 direct neighbour.

r_8 = correlation between subject tree X and 1 diagonal neighbour.

r_9 = correlation between subject tree X and 1 direct or diagonal neighbour.

r_{10} = correlation between subject tree X and number of missing values among the 4 direct neighbours.

r_{11} = correlation between subject tree X and number of missing values among the 4 diagonal neighbours.

r_{12} = correlation between subject tree X and number of missing values among the 8 direct and diagonal neighbours.

All these correlation coefficients are calculated as simple phenotypic correlations based on the individual phenotypic measurements.

The simultaneous calculation of the spatial correlations between the subject tree and the sum as well as the mean of its competing neighbours provides a very rough assessment of effects of missing values and nonregular patterns. Both correlations must be identical for constant numbers of competing
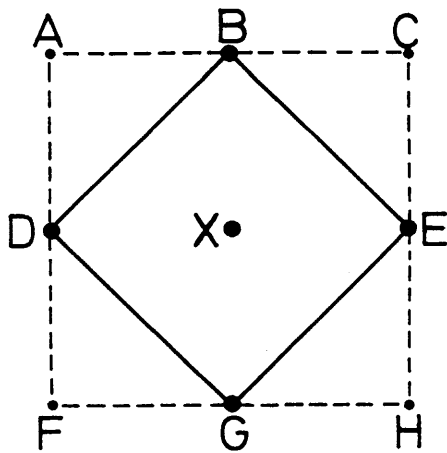
Figure 1. – Competing neighbours (direct and diagonal) for the subject tree X.

neighbours. Equal sums of neighbouring measurements can be obtained from different numbers of competing neighbours (= different means) while, on the other side, equal means may be obtained by different sums. Differences between both spatial correlations (sum, mean), therefore, are indicative for such effects of nonregular patterns caused by missing neighbours.

The calculation and interpretation of the correlation coefficients r_{10}, r_{11}, and r_{12} should be handled very cautiously: The discrete variable "number of missing values", of course, doesn't fulfill the requirements for a common correlation analysis. In this study, these correlations have been only calculated incidentally in a purely formal-descriptive point of view to detect dependencies between trait measurements and numbers of missing neighbours.

The plant material of this field trial consists of 27 entries which can be divided into 3 groups of entries (*Larix europaea, Larix leptolepis,* and their hybrids). In the present investigations, however, no separate calculation of the correlation coefficients r_1, r_2, ..., r_{12} for individual entries or for groups of entries have been carried out. All correlation coefficients in this study are based on the collected total plant material. A discussion of the spatial correlation patterns for individual entries or for groups of entries will be published elsewhere.

Tests of significance for the diverse correlation coefficients were carried out by standard procedures from elementary statistics. Since the calculated correlation coefficients are based on very large numbers of values, very small correlation coefficients and very small differences between correlation coefficients are significant: Deviations from zero of a correlation coefficient r_i can be tested by the test statistic $[r_i^2(n-2)/(1-r_i^2)]^{1/2}$ which is t-distributed with n-2 degrees of freedom where n denotes the sample size. The lowest number n for all correlation coefficients from *tables 2* and *3* is n = 1081. For an error probability α of α = 10% and for n = 1081, a r_i-value as small as 0.05 is significantly different from zero (r_i = 0.06 for α = 5% and r_i = 0.08 for α = 1%).

Similar conclusions are obtained for the comparison of 2 correlation coefficients r_i and r_j if one applies FISHER's z-transformation

$$z = \frac{1}{2} \ln \frac{1+r}{1-r} .$$

The difference $r_i - r_j$ can be tested by the test statistic

$$(z_i - z_j) / \left(\frac{1}{n_i - 3} + \frac{1}{n_j - 3} \right)^{1/2}$$

which is standard normally distributed where n_i and n_j are the two sample sizes. The lowest and the second lowest sample sizes for all correlation coefficients from *tables 2* and *3* are $n_i = 1081$ and $n_j = 1089$. For α = 10% and these 2 sample sizes the correlation coefficients r_i and r_j are significantly different if $|z_i - z_j| \geq 0.07$ ($|z_i - z_j| \geq 0.08$ for α = 5% and $|z_i - z_j| \geq 0.11$ for α = 1%). Two correlation coefficients r_i and r_j are, therefore, significantly different for α = 10%, if they differ by more than 0.07 (0.08 for α = 5% and 0.11 for α = 1%).

Results and Discussion

The numerical values of the correlation coefficients are presented in *table 2* (height), *table 3* (diameter) and *table 4* (individual basal area). The main results are:

For "height" (Table 2)

1. The signs of the diverse correlation coefficients exhibit a quite uniform pattern: r_1, r_2, ..., r_9 are positive for all ages, while r_{10}, r_{11} and r_{12} are negative for all ages. Since all entries are planted in plots, each individual subject tree is surrounded by competing neighbours which belong to the same entry (exception: subject trees at the borders of the plots with competing neighbours belonging to other entries). Subject trees of a high-yielding entry are, therefore, mostly surrounded by high-yielding neighbours and subject trees of a low-yielding entry are mostly surrounded by low-yielding neighbours. If one calculates the neighbourhood correlation coefficients for the combined data sets of the measurements for all entries, the positive values of r_1, r_2, ..., r_9 must be expected.

Table 2. – Correlation coefficients r_1, r_2, ..., r_{12} for height at the 5 stages of stand development.

corre-lation	stages of stand development = ages (in years)									
	11	size	13	size	18	size	19	size	50	size
r_1	0.39	1308	0.40	1281	0.42	1249	0.42	1205	0.22	1139
r_2	0.32	1246	0.32	1226	0.35	1192	0.37	1144	0.18	1081
r_3	0.40	1337	0.41	1317	0.44	1281	0.46	1236	0.26	1186
r_4	0.53	1308	0.54	1281	0.57	1249	0.62	1205	0.58	1139
r_5	0.53	1246	0.52	1226	0.56	1192	0.62	1144	0.51	1081
r_6	0.59	1337	0.59	1317	0.62	1281	0.67	1236	0.61	1186
r_7	0.45	3401	0.46	3282	0.49	3181	0.56	2970	0.50	2634
r_8	0.45	2881	0.45	2804	0.49	2706	0.55	2524	0.43	2272
r_9	0.45	6282	0.46	6086	0.49	5887	0.56	5494	0.47	4906
r_{10}	-0.24	1342	-0.26	1323	-0.28	1292	-0.28	1249	-0.12	1197
r_{11}	-0.21	1342	-0.22	1323	-0.26	1292	-0.27	1249	-0.15	1197
r_{12}	-0.26	1342	-0.28	1323	-0.31	1292	-0.32	1249	-0.17	1197
height - diameter	0.88	1342	0.88	1323	0.86	1292	0.83	1249	0.34	1197

The negative values for r_{10}, r_{11}, and r_{12} indicate increasing trait measurements with a decreasing number of missing trees in the neighbourhood. In this wide-spacing trial, therefore, a regular and complete configuration of competing neighbours supports a more ore less undisturbed development of height growth. The correlation coefficients r_{10}, r_{11}, and r_{12}, however, are numerically low (approximately - 0.15 at age 50).

This more or less undisturbed development of height growth, however, don't coincide with optimal height growth. The graphs of height growth dependent on space per tree are clear optimum curves, where the maxima (= optima) are obtained for much closer spacings (see, for example, DIPPEL, 1982).

2. The correlation coefficients r_1, r_2 and r_3 slightly increase from age 11 up to age 19, but then drastically decrease up to age 50. The correlations at age 50 are approximately 0.20.

3. For each age one obtains the relationship:

$$r_2 < r_1 < r_3 \tag{1}$$

That means: The correlation between a subject tree and the sum of its diagonal neighbours is lowest and the correlation between a subject tree and the sum of all neighbours (direct and diagonal) is largest. The correlation between a subject tree and the sum of its direct neighbours is intermediate. The correlation coefficients r_3 and r_1, however, are numerically quite similar. These results are in line with the theoretical expectations which are based on purely spatial considerations.

4. The correlation coefficients r_4, r_5 and r_6 slightly increase from age 11 up to age 19, followed by an only minor decrease up to age 50. The correlations between a subject tree and the means of its competing neighbours (direct, diagonal, total) are, therefore, approximately constant over the entire period of measurements from age 11 up to age 50.

5. For the correlations with the means of the competing neighbours one obtains the same relationship as for the correlations with the sums of the competing neighbours, i. e. for each age it is:

$$r_5 < r_4 < r_6 \tag{2}$$

The correlation is lowest for the mean of the diagonal neighbours, largest for the mean of all neighbours (direct and diagonal) and intermediate for the mean of the direct neighbours. r_5 and r_4 are numerically similar (slight exception: age 50), while r_6 is considerably larger than both coefficients.

6. The correlations based on the means of the competing neighbours (direct, diagonal, total) are much larger than the correlations based on the sums of the competing neighbours (direct, diagonal, total):

$$r_1 < r_4; \; r_2 < r_5; \; r_3 < r_6 \tag{3}$$

These relationships are valid for each age.

7. The relationships (1) and (2) can be combined to:

$$r_2 < r_1 < r_3 < r_5 < r_4 < r_6 \tag{4}$$

These inequalities are true for each age.

8. For each age, the values of the correlations r_7, r_8 and r_9 are numerically identical (slight exception: age 50). These correlations slightly increase from age 11 to age 19 and then moderately decrease up to age 50.

9. The negative correlations r_{10}, r_{11} and r_{12} are very similar in their numerical magnitude (for each age). Their absolute values slightly increase from age 11 up to age 19 and then considerably decrease up to age 50. The final value at age 50 is approximately -0.15.

10. For the absolute values of the correlations r_{10}, r_{11} and r_{12} one obtains the relationship:

$$|r_{11}| < |r_{10}| < |r_{12}| \tag{5}$$

This result is valid for each age (slight exception: age 50).

The correlation coefficients from *table 2* are based on very large numbers of observations. All these correlation coefficients are, therefore, significantly different from zero.

For "diameter" (Table 3)

1. The signs of the diverse correlation coefficients show a quite characteristic pattern: r_1, r_2 and r_3 are positive for ages 11 up to 19 and negative for ages 42 up to 50, while the correlation coefficients r_{10}, r_{11} and r_{12} exhibit the reverse pattern: negative for ages 11 up to 19 and positive for ages 42 up to 50. The correlations r_4, r_5, ..., r_9 are positive for all ages.

If one applies the same explanations and expectations as for height in No. 1 of the previous section, the negative correlations r_1, r_2 and r_3 for the later ages and the positive correlations r_{10}, r_{11} and r_{12} for the later ages must be otherwise explained. Both deviating phenomena, however, are due to the following evident relationship: In the early periods of stand development the individual trees of this wide-spacing trial exhibit a more or less undisturbed diameter growth. With increasing age the competition pressure increases and considerable competitive effects appear in only advanced stages of stand development. Diameter reacts much more sensitive to competitive effects than height. An increasing number of missing competing neighbours reduces the competitive pressure. The subject tree responds with larger values for the trait diameter leading to positive correlations for r_{10}, r_{11} and r_{12}.

Such effects, however, are of practical relevance for an only limited range of stand densities. The graphs of diameter growth dependent on space per tree are clear saturation curves where the final asymptotic numerical niveau is obtained for relatively close spacings (see, for example, DIPPEL, 1982).

An increasing number of missing competing neighbours, however, coincides with decreasing sums of the competing neighbours. The correlation coefficients r_1, r_2 and r_3, therefore, must be negative. These findings are in line with the well-known competition-sensitivity of the trait diameter.

Because of this clear distinction between early and late periods of stand development, the subsequent discussion of the numerical values of the diverse correlation coefficients has been separately carried out for early (11 to 19) and late (42 to 50) periods.

2. The correlations r_1, r_2 and r_3 slightly decrease from age 11 up to age 19, but then drastically change their sign and numerical magnitude from age 42 up to age 50.

3. For each age in the "early period" (11 to 19 years), with positive correlations r_1, r_2 and r_3, one obtains:

$$r_2 < r_1 < r_3 \tag{6}$$

Table 3. – Correlation coefficients r_1, r_2, ..., r_{12} for diameter at the 7 stages of stand development.

stages of stand development = ages (in years)

corre-lation	11	size	13	size	18	size	19	size	42	size	49	size	50	size
r_1	0.41	1308	0.38	1281	0.33	1249	0.32	1205	-0.21	1151	-0.26	1141	-0.27	1139
r_2	0.35	1249	0.32	1225	0.29	1192	0.30	1143	-0.05	1089	-0.08	1081	-0.08	1081
r_3	0.42	1337	0.39	1317	0.36	1281	0.37	1235	-0.17	1196	-0.22	1187	-0.24	1186
r_4	0.49	1308	0.49	1281	0.44	1249	0.45	1205	0.14	1151	0.13	1141	0.14	1139
r_5	0.46	1249	0.46	1225	0.40	1192	0.41	1143	0.14	1089	0.12	1081	0.13	1081
r_6	0.53	1337	0.53	1317	0.48	1281	0.50	1235	0.18	1196	0.16	1187	0.18	1186
r_7	0.41	3401	0.40	3282	0.36	3181	0.38	2969	0.10	2677	0.10	2631	0.10	2633
r_8	0.38	2878	0.37	2803	0.32	2706	0.35	2521	0.10	2299	0.11	2265	0.11	2273
r_9	0.40	6279	0.39	6085	0.34	5887	0.37	5490	0.10	4976	0.10	4896	0.11	4906
r_{10}	-0.21	1342	-0.21	1323	-0.21	1292	-0.21	1249	0.24	1208	0.30	1198	0.31	1197
r_{11}	-0.21	1342	-0.19	1323	-0.21	1292	-0.24	1249	0.07	1208	0.11	1198	0.12	1197
r_{12}	-0.25	1342	-0.23	1323	-0.25	1292	-0.27	1249	0.19	1208	0.25	1198	0.26	1197

while for the "late period" (42 to 50 years), with negative correlations r_1, r_2 and r_3, the relationships are changed to:

$$|r_2| < |r_3| < |r_1| \qquad (7)$$

In both periods (early, late), however, the correlation coefficients r_1 and r_3 are more or less similar, while the correlation coefficient r_2 is considerably smaller in its absolute numerical amount.

4. The correlation coefficients r_4, r_5 and r_6 slightly decrease from age 11 up to age 19, but then attain a numerical plateau at age 42 with approximately constant numerical values up to age 50 ($r_4 = 0.14$, $r_5 = 0.13$ and $r_6 = 0.18$).

5. For the correlations between a subject tree and the means of its competing neighbours one obtains:

$$r_5 < r_4 < r_6 \text{ (for each age)} \qquad (8)$$

The correlation is lowest for the mean of the diagonal neighbours, largest for the mean of all neighbours (direct and diagonal) and intermediate for the mean of the direct neighbours. For the "late" period (42 to 50 years), however, the correlations r_4 and r_5 are practically identical.

6. For the "early" period (11 to 19 years): The correlations based on the means of the competing neighbours (direct, diagonal, total) are much larger than the correlations based on the sums of the competing neighbours (direct, diagonal, total):

$$r_1 < r_4; r_2 < r_5; r_3 < r_6 \qquad (9)$$
(for each age)

7. For the "early" period, a combination of (6) and (8) leads to:

$$r_2 < r_1 < r_3 < r_5 < r_4 < r_6 \qquad (10)$$
(for each age)

8. For each age (in the "early" and "late" period), the correlations r_7, r_8 and r_9 are very similar.

For the "late" period these values are practically identical. In the "early" period, these correlations slightly decrease from age 11 onwards (with $r_8 < r_9 < r_7$). At age 42 these values have been drastically reduced to a constant numerical plateau of 0.10 which is maintained up to age 50.

9. For the "early" period (11 to 19 years): The negative correlations r_{10}, r_{11} and r_{12} are similar in their numerical magnitude (for each age) with practically identical values for r_{10} and r_{11} and a slightly stronger (negative) correlation r_{12}.

For the "late" period (42 to 50 years) the correlations r_{10}, r_{11} and r_{12} are positive (for all ages). Each correlation slightly increases from age 42 up to age 50.

10. For each age from the "late" period the following relationship holds:

$$r_{11} < r_{12} < r_{10} \qquad (11)$$

The correlation coefficients r_{10}, r_{11} and r_{12} are considerably different from each other.

All correlation coefficients from *table 3* are based on very large numbers of observations. All the values are, therefore, significantly different from zero.

For "individual basal area" (Table 4)

A commonly used measure for the yield level of entries or stands is the sum of the individual basal areas at breast height [$\pi(D/2)^2$ with D = diameter at breast height] of all living trees expressed in the unit m²/ha. In this study, however, we are not interested in yield levels, but in correlations between neighbouring individual trees. In this section we, therefore, analyse basal area as a separate trait of individual trees. Since the correlation patterns for diameter and for individual basal area must be similar in their basic characteristics, no detailed

discussion of the results for individual basal area (*Table 4*) shall be presented. Here, we only point to the most worth mentioning differences:

Table 4. – Correlation coefficients r_1, r_2, ..., r_{12} for individual basal area at the 7 stages of stand development.

corre-lation	stages of stand development = ages (in years)						
	11	13	18	19	42	49	50
r_1	0.49	0.47	0.40	0.39	-0.17	-0.21	-0.23
r_2	0.44	0.40	0.36	0.36	-0.02	-0.05	-0.04
r_3	0.50	0.47	0.43	0.43	-0.13	-0.19	-0.20
r_4	0.52	0.52	0.47	0.47	0.15	0.13	0.14
r_5	0.49	0.48	0.43	0.42	0.15	0.13	0.14
r_6	0.56	0.56	0.50	0.51	0.18	0.16	0.18
r_7	0.44	0.43	0.37	0.39	0.11	0.11	0.11
r_8	0.40	0.39	0.34	0.35	0.11	0.11	0.12
r_9	0.42	0.41	0.36	0.37	0.11	0.11	0.12
r_{10}	-0.21	-0.20	-0.21	-0.21	0.26	0.30	0.32
r_{11}	-0.21	-0.19	-0.21	-0.23	0.08	0.11	0.12
r_{12}	-0.25	-0.23	-0.24	-0.26	0.21	0.26	0.27
height - individual basal area	0.84	0.83	0.83	0.81	-	-	0.33

1. The correlation between height and diameter is slightly stronger than the correlation between height and individual basal area.

2. For the "early" period (11 to 19 years): The correlations r_{10}, r_{11} and r_{12} are practically identical for diameter and for individual basal area, while the correlations r_4, r_5, ... and r_9 are slightly stronger for individual basal area than for diameter. The correlations r_1, r_2 and r_3, however, are clearly stronger for individual basal area than for diameter.

3. For the "late" period (42 to 50 years): The correlations r_4, r_5, ... and r_{12} are practically identical for diameter and for individual basal area. The correlations r_1, r_2 and r_3, however, are clearly stronger for diameter than for individual basal area.

In this paper, the aforementioned results on the relationships between the correlation patterns for diameter and for individual basal area have been obtained by the analysis of empirical data sets. Theoretical investigations on these topics can be easily carried out by utilizing the functional relationship between diameter and individual basal area. These theoretical investigations, however, will be published elsewhere.

Comparison "height-diameter"

For ages 42 and 49 only diameter measurements are available. Comparisons between the spatial neighbourhood correlation patterns for height and diameter, therefore, can be only carried out for the ages 11, 13, 18, 19, and 50. The main results are:

1. The correlation between height and diameter is very strong and approximately constant in the "early" period (11 to 19 years) with an only slight decrease from age 11 (correlation = 0.88) up to age 19 (correlation = 0.83). But, then the correlation decreases drastically up to age 50 (correlation = 0.34) (*Table 2*), i. e. the strong relationship between height and diameter disappears during stand development.

Based on these facts, one may expect different spatial neighbourhood correlation patterns for height and diameter between "early" and "late" periods of measurements.

2. A comparison of the signs of the correlation coefficients reveals the basic differences in the correlation patterns for height and diameter. These signs are presented in *table 5*. The patterns of signs for height and diameter are identical for the "early" period (11 to 19 years). Differences were only observed

Table 5. – Signs of correlation coefficients r_1, r_2, ..., r_{12} for height and for diameter/individual basal area.

corre- lation	height					diameter/individual basal area						
	11	13	18	19	50	11	13	18	19	42	49	50
r_1	+	+	+	+	+	+	+	+	+	-	-	-
r_2	+	+	+	+	+	+	+	+	+	-	-	-
r_3	+	+	+	+	+	+	+	+	+	-	-	-
r_4	+	+	+	+	+	+	+	+	+	+	+	+
r_5	+	+	+	+	+	+	+	+	+	+	+	+
r_6	+	+	+	+	+	+	+	+	+	+	+	+
r_7	+	+	+	+	+	+	+	+	+	+	+	+
r_8	+	+	+	+	+	+	+	+	+	+	+	+
r_9	+	+	+	+	+	+	+	+	+	+	+	+
r_{10}	-	-	-	-	-	-	-	-	-	+	+	+
r_{11}	-	-	-	-	-	-	-	-	-	+	+	+
r_{12}	-	-	-	-	-	-	-	-	-	+	+	+
	'early' period				'late' period	'early' period				'late' period		

for age 50: Here, the correlation coefficients r_1, r_2 and r_3 are positive for height and negative for diameter, while the reverse is true for the correlation coefficients r_{10}, r_{11} and r_{12} which are negative for height and positive for diameter (Table 5).

Height is less influenced by competition than diameter. With increasing age the competitive pressure increases, i. e.:

In advanced stages of stand development a subject tree responds to a decreasing competitive pressure (= increasing number of missing competitive neighbours) with larger diameter values, i. e. the correlations r_{10}, r_{11} and r_{12} are positive. But, simultaneously, the height values decrease, i. e. the correlations r_{10}, r_{11} and r_{12} are negative. That means, in these situations the subject tree reacts with an improved diameter growth, but not with an improved height growth.

The correlation coefficients r_{10}, r_{11} and r_{12} for age 50, however, are numerically small (for height and for diameter). Furthermore, the correlation between height and diameter for age 50 is also small (correlation = 0.34). Because of these weak relationships for advanced stages of stand development and, particularly, because of the very wide spacing of this field trial, no clear and cogent silvicultural consequences can be established and justified by these experimental results on spatial correlation patterns. Such implications with relevance for silvicultural practices may be obtained by a more refined and sophisticated analysis of spatial neighbourhood correlation patterns, for example by a separate analysis for each individual entry. These specified results will be published in a separate paper.

3. For each age from the "early" period of measurements (11 to 19 years) the correlation coefficients for height and diameter are identical in sign and not too different in their numerical amount. This result is valid for each r_i, i = 1, 2, ..., 12. In almost all cases one obtains a stronger relationship for height than for diameter.

For the "late" period, a comparison between height and diameter can be only carried out for age 50 where both correlation coefficients are quite different for each r_i, i = 1, 2, ..., 12. Additional ages (> 50) should be analysed to see whether or not the correlation coefficients for age 50 can be considered as a numerical plateau or if there are further changes of the correlations.

The preceding investigations are based on several simplifying assumptions. A critical discussion of the numerical results on spatial neighbourhood correlation patterns primarily must be concerned with the possible limitations and restrictions of these results imposed by the different assumptions.

In the analysis of irregular neighbourhood configurations caused by a varying number and position of missing neighbours no consideration has been taken into account at which point in time these missing neighbours appeared during stand development. It will be, of course, of importance for the resulting correlation patterns whether these neighbours fail shorter or longer before a certain time of measurement. An explicit consideration of such effects has been excluded from the analyses. This aspect is of particular importance for an interpretation of the results for height at age 50 since there exists a long time interval to the precedent measurement at age 19. The reduction in the number of trees from age 19 up to age 50, however, is approximately only 4 %. So, these biasing effects may be not too severe.

There are some further criticisms with regard to the statistical point of view: For the calculation of r_7, for example, the same subject tree measurement has been related to each of its 4 direct neighbours (Fig. 1), that means: the same numerical value is included fourfold for the calculation of r_7 by simultaneously using the pairs (X, E), (X, G), (X,D) and (X,B). In the strict statistical sense, these four values X cannot be considered as independent realizations of a random variable. The same criticism, of course, is due to r_8 and r_9.

Another critical comment is related to the reciprocal neighbourship of adjacent individuals (Fig. 1): E is a direct neighbour to X and X is a direct neighbour to E. For the calculation of the correlation between subject tree and one direct neighbour the measurements for trees X and E are included twice by using both pairs (X,E) and (E,X) simultaneously. Again, some statistical difficulties may be involved.

But, we think that these statistical arguments impose no severe limitations with regard to the objectives of this paper. No statistical methodology which sensitively depends on violated assumptions has been applied. All the investigations of this study have been primarily carried out in a purely descriptive approach to detect formal correlative relationships inherent in the data sets. This "descriptive analysis" seems to be unaffected by this sophisticated statistical criticism.

All correlation coefficients in this paper have been calculated for the collected total material. No separate calculations have been carried out for individual entries. For quite inhomogeneous individual data sets it is well known that a clear correlation can be obtained for the summarized total material while no correlation exists for each individual sub-dataset. Whether or not such inhomogeneity effects may be involved in the ex-

planation of the numerical amount of the diverse correlation coefficients in this paper will be discussed elsewhere.

Main Conclusions

With regard to silvicultural applications the practioneer, of course, is mainly interested in later stages of stand development. In this point of view, the previous results for age 50 must be of particular interest.

. .A comparison of spatial neighbourhood correlations for height and for diameter at age 50 should be restricted to a discussion of r_7, r_8 and r_9. These coefficients are those neighbourhood correlations which are based on pairs of individual neighbouring trees while the remaining correlations are based on sums of neighbours, means of neighbours or numbers of missing neighbours. The correlations r_7, r_8 and r_9 are, therefore, accessible to direct biological interpretations (competitive pressure by sharing common resources within the stand).

A comparison of these spatial neighbourhood correlation coefficients for height and for diameter at age 50 reveals clearly stronger relationships for height than for diameter.

The strongest relationship for height at age 50 is the correlation r_7 ($r_7 = 0.50$) (= correlation between a subject tree and one direct neighbour). The correlation between a subject tree and one neighbour (direct or diagonal), however, is only slightly smaller ($r_9 = 0.47$) while the correlation between a subject tree and one diagonal neighbour is lowest ($r_8 = 0.43$). The different spatial neighbourhoods (direct neighbours, diagonal neighbours, all neighbours) are, therefore, of only minor influence on the numerical amount of the resulting neighbourhood correlations.

The correlation coefficients r_7, r_8 and r_9 for diameter at age 50 are practically constant with a numerical value of 0.11. For this trait, the different spatial neighbourhoods are of no differential influence on the numerical amount of the resulting neighbourhood correlations.

Expressed in the regression point of view, the previous results can be very roughly summarized as: 25% of the variability in the trait height can be explained by a dependence on the height measurements of the neighbouring trees, while this percentage is reduced to only 1% for the trait diameter.

The silvicultural consequences of these findings as well as the implications for forest tree improvement programs are obvious.

Acknowledgement

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Investigations on the Correlation Pattern in Even-Aged Stands of Larch

III. Static Description of Phenotypic Correlations Between Neighbouring Observations[1])

By W. Langner[2]) and M. Hühn[3])

Summary

The main topic of this study is a static description of spatial neighbourhood correlation patterns of stands of larch, i. e. an analysis of the correlations between neighbours at only one point in time. For these investigations extensive data sets from 9 field trials with a varying number (8 to 23) of "entries" (*Larix europaea, Larix leptolepis*, hybrids) have been used. The trials are slightly different in their ages (7 to 11 years). Single tree measurements of these trials were available for the traits height and diameter at breast height. Additionally, the diameter values have been transformed and analysed as individual basal areas.

The correlative structure of these trials for measurements of neighbouring individuals (regular square spacing with spacings 1.5 m x 1.5 m, artificial thinning procedures for only 2 of the trials) has been described by 12 different correlation coefficients. These coefficients are defined by considering quite different spatial configurations of competitive neighbourhoods. In these procedures and analyses the diagonally located neighbours of a subject tree and its missing neighbours too are explicitly considered.

For the trait height one obtains for all trials a quite uniform correlation pattern: positive correlations with intermediate or small numerical amount between the trait measurement of a subject tree and the corresponding value of its neighbourhood (for different spatial definitions of neighbourhood) and negative correlations of similar numerical amount between the trait measurement of a subject tree and the number of missing neighbours in its neighbourhood.

The correlations for the trait diameter are throughout very small. In most of the field trials one obtains stronger spatial neighbourhood relationships for height than for diameter.

The correlation between height and diameter varies between 0.63 and 0.94. This correlation, therefore, exhibits a considerable variability. The estimates of the correlation coefficients as well as the detected relationships are of high reliability since the correlation calculations of this study are based on large numbers of observations (smallest sample size = 199, largest sample size = 6649).

Zusammenfassung

Für die statische Betrachtung des räumlichen Korrelationsmusters von Lärchenbeständen, d. h. für die einmalige Analyse der Nachbarschaftskorrelationen eines Bestandes zu einem bestimmten Zeitpunkt seiner Entwicklung, wurden 9 Versuchsflächen mit einer unterschiedlichen Anzahl (8 bis 23) an „Sorten" (Europalärchen, Japanlärchen, Hybriden) ausgewählt, die zu etwas verschiedenen Altersstufen (7 bis 11 Jahre) einzelbaumweise vermessen wurden. Die erhobenen Merkmale sind „Höhe" und „Durchmesser". Zusätzlich werden die Durchmesserwerte transformiert und als individuelle Grundflächen ausgewertet.

Die Nachbarschafts-Korrelationsstruktur der im quadratischen 1,5 m x 1,5 m Verband angelegten und (mit Ausnahme zweier Flächen) auch nichtdurchforsteten Lärchenbestände wird durch 12 verschiedene Korrelationskoeffizienten beschrieben, die durch die Heranziehung von unterschiedlichen räumlichen Nachbarschaftskonfigurationen definiert werden. Dabei werden auch diagonal entfernt stehende Nachbarn sowie auch fehlende Nachbarn explizit in die Ansätze und Auswertungen mit einbezogen.

Für das Merkmal „Höhe" erhält man für sämtliche Versuche ein sehr übereinstimmendes Korrelationsmuster: positive Korrelationen mittlerer bis geringer numerischer Höhe zwischen dem Merkmalswert eines Baumes und dem entsprechenden Wert für seine Nachbarschaft (bei unterschiedlichen räumlichen Definitionen von Nachbarschaft) und negative Korrelationen vergleichbarer Größenordnung zwischen dem Merkmalswert eines Baumes und der Anzahl Fehlstellen in seiner Nachbarschaft.

Die Korrelationen für das Merkmal „Durchmesser" sind durchweg sehr gering. In den meisten Versuchen ergeben sich für „Höhe" straffere räumliche Nachbarschaftskorrelationen als für „Durchmesser".

Die Korrelation zwischen „Höhe" und „Durchmesser" schwankt zwischen 0,63 und 0,94 und zeigt somit eine beträchtliche Variationsbreite.

Den geschätzten Korrelationskoeffizienten sowie den zwischen ihnen aufgefundenen Größenbeziehungen kommt eine hohe Zuverlässigkeit zu, da diese Korrelationsberechnun-

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[1]) Dedicated to Dr. G. H. Melchior on his 70th birthday.

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