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Spatial Stand Structure of Sugar Maple (*Acer saccharum* Marsh.) in Ontario, Canada

By

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With 2 Figures

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Summary

GEBUREK TH. & TRIPP-KNOWLES P. 1994. Spatial stand structure of sugar maple *(Acer saccharum)* in Ontario, Canada. – Phyton (Horn, Austria) 34 (2): 267–278, with 2 figures. – English with German summary.

In *Acer saccharum*, the spatial distribution of tree size and individual response to environmental stress was investigated by means of spatial autocorrelation. Within 106 mature sugar maple stands in Ontario, Canada, traits of 7856 trees were analyzed.

Evidence of this study supports the hypothesis that, in old forest stands, trees of similar size are found in patches. Significant spatial autocorrelation was detected for 57 % of all forest stands for at least one distance class and 25 % of the correlograms indicated non random spatial pattern. As expected, spatial distribution of tree diameter growth was similar to height patchiness; for 50 % of the maple stands Moran's *I*-values for one or more distance classes and 9% of the spatial correlograms were significant. Both for height and diameter growth, spatial coefficients were predominantly positive for short distances and negative for long distances. Patch size extension for trees having similar size was approximately 15–25 m. Despite non spatial randomness of individual response to environmental stress could be antici-

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pated due to certain causes significant clusters were not found in sugar maple stands.

Rank correlations between MORAN's *I*-values and descriptive stand variables (age, basal area, height, tree density) were not significant whereas clumping of tree size was more pronounced in stands with less crown closure. For future investigations, study sites should comprise approximately 300–400 trees. This study shows that spatial autocorrelation analysis can potentially provide useful information for an enhanced ecological assessment of forest stand development.

Zusammenfassung

GEBUREK TH. & TRIPP-KNOWLES P. 1994. Räumliche Bestandesstruktur beim Zuckerahorn (*Acer saccharum* Marsh.) in Ontario, Kanada. – Phyton (Horn, Austria) 34 (2): 267–278, 2 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Räumliche Strukturen wurden in *Acer saccharum*-Beständen für die Merkmale Baumgröße und Respons auf Umweltstreß anhand Verfahren der räumlichen Autokorrelation untersucht. Felddaten von 7856 Bäumen aus 106 Beständen in Ontario, Kanada, wurden analysiert.

Die Ergebnisse unterstützen die Hypothese, daß in alten, natürlichen Beständen Bäume mit ähnlicher Größe in Clustern auftreten. Für das Merkmal Baumhöhe wurden signifikante räumliche Autokorrelationen, zumindest für eine Distanzklasse, in 57 % der Bestände gefunden. Räumliche Korrelogramme waren zu 25 % signifikant. Das räumliche Verteilungsmuster für den Zuwachs des Stammdurchmessers war dem der Baumhöhe erwartungsgemäß ähnlich; 50 % der MORANschen Korrelationen für eine oder mehrere Distanzklassen bzw. 9 % der Korrelogramme waren signifikant. Für beide Merkmale (Baumhöhe und Zuwachs) waren die Autokorrelationskoeffizienten in Kurzdistanzklassen positiv und in Langdistanzklassen negativ. Für die Cluster mit Bäumen ähnlicher Größe wurden Durchmesser geschätzt, die zwischen 15 und 25 m variierten. Obwohl räumliche Cluster von Bäumen mit ähnlicher Respons auf Umweltstreß aufgrund verschiedener Ursachen erwartet werden konnten, bestand ein zufälliges räumliches Verteilungsmuster für dieses Merkmal in den Zuckerahornbeständen.

Zwischen MORANschen *I*-Werten und deskriptiven Bestandesvariablen (Alter, Bestandesgrundfläche, Bestandeshöhe, Bestandesdichte) bestanden keine signifikanten Rankkorrelationen. Hingegen waren Cluster für das Merkmal Baumgröße in Beständen mit geringem Dichtschluß der Baumkronen ausgeprägter als in Beständen mit hohem Kronendichtschluß. Für künftige Untersuchungen sollten analysierte Bestände ca. 300–400 Bäume aufweisen. Die vorliegende Arbeit zeigt, daß Verfahren der räumlichen Autokorrelation potentiell zur ökolischen Evaluierung von Waldbeständen beitragen können.

Introduction

Since the first studies of non-random dispersion of plant species in an apparent uniform environment (*e.g.*, GLEASON 1920), spatial analyses have provided intriguing insights into ecological structures. In forests, the distribution of many tree species is clumped at a small scale (GILL 1975, RICHARDS & WILLIAMSON 1975, ABBOTT 1984, NASI 1993, see also

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SZWAGRZYK 1990). For above-mentioned studies, the distribution of different species or tree traits in space, *i.e.*, the distribution of points in space, has been the object. Quadrat analyses (PIELOU 1977) and their derivatives (HAMILL & WRIGHT 1986, GETIS & FRANKLIN 1987) have been often employed to assess this type of spatial structure. Compared to many studies using quadrat analyses, only a few have reported evidence of spatial structure in trees using spatial autocorrelation. In contrast to quadrat analysis, spatial autocorrelation analysis does not ask if a character is randomly distributed in space in relation to geographic distances, but if a trait is randomly distributed in space in relation to the actual point pattern.

DUNCAN & STEWART 1991 used spatial autocorrelation analysis to enhance the interpretation of tree disturbance history and tree regeneration patterns in a *Dacrycarpus dacrydioides* stand and a mixed *Nothofagus fusca* forest. Spatial autocorrelation analysis has been also employed to assess spatial growth pattern in a forest based on field and simulated data in loblolly pine (*Pinus taeda*) (REED & BURKHART 1985). So far, their postulate of positive autocorrelation in older stands has only been confirmed in a single silver maple (*Acer saccharinum*) stand (SAKAI & ODEN 1983). Knowledge of spatial pattern of tree size and of other quantitative traits, such as tree damage, is still very limited, however.

In the present study, the spatial autocorrelation of sugar maple (*Acer saccharum* Marsh.) has been investigated. This hardwood species is of great ecological and commercial importance in deciduous forests of Eastern Canada and the Great Lakes States (GODMAN & al. 1990). By using spatial autocorrelation analysis, the spatial patterns of tree size (height, stem diameter) and of individual tree response due to environmental stress (unknown in detail) were analyzed in 106 mature stands in Ontario, Canada. Particular attention is given to the following questions: (i) Is the spatial pattern based on tree size non-random, and if so, what is the spatial structure? (ii) Do damaged trees occur in clumps or are they randomly distributed over space? (iii) Is the spatial pattern of different tree traits correlated with descriptive stand characteristics?

Materials and Methods

Species and study sites

Acer saccharum is one of the largest and most important of the hardwoods in the eastern half of the United States of America and Canada. This relatively windfirm species occurs in a wide range often in fertile, moist, well-drained, and moderately acid sites. It is very tolerant to shade and is able to withstand several years of complete suppression by other trees, caused by crown overshading (GODMAN & al. 1990).

Measurements taken from 7,856 trees at 106 sugar maple stands throughout Ontario, Canada, were used (Fig. 1). The sites are part of an ongoing hardwood decline survey conducted on behalf of the Ontario Ministry of the Environment. Spe-

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Fig. 1

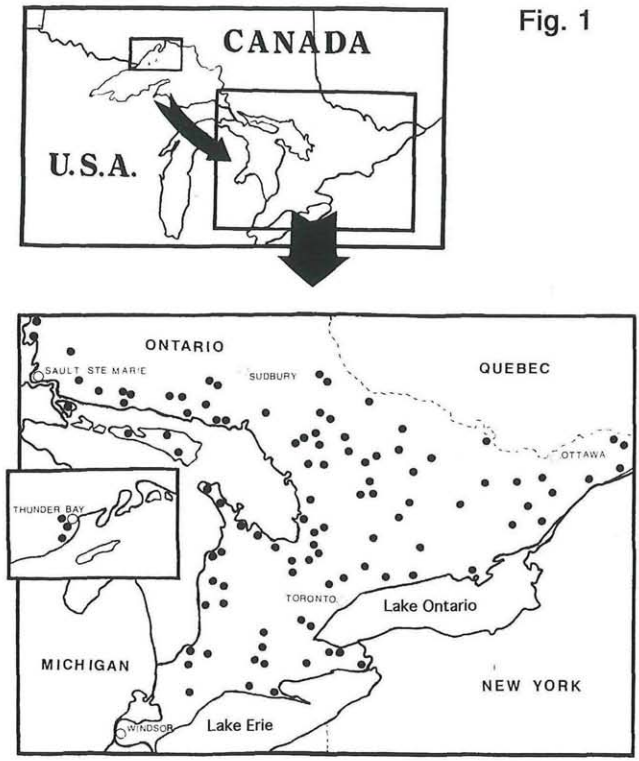

Fig. 1. Map showing locations of *Acer saccharum* study sites (•) in Ontario, Canada.

cific criteria for the site selection were high density of sugar maple (> 50% of cover), large stand size (> 10 ha), and advanced age (> 75 years). Each study site was characterized by several stand characteristics such as age, basal area, percentage of crown closure, and tree density compared to the expected basal area given in yield tables for the respective age of the single stands (PLONSKI 1981). Raw data for this study were supplied by the Ministry of the Environment, Ontario, Canada.

Data

At each site, an engineer's transit was set up over the site centre post. One hundred trees greater than 10 cm (diameter at breast height) were then located and mapped. Total height and diameter at breast height were recorded. To assess the response of each tree to environmental stress a series of subjective tree crown ratings of decline indicators (percentages of dead branches, undersized leaves, strong and slight chloroses) common in Ontario were employed (MCILVEEN & al. 1989).

For each tree, following data were analyzed: height, diameter at breast height (dbh), and individual decline. Tree response to environmental stress was assessed according a decline index (DI) (MCILVEEN & al. 1989) which was based on the per-

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centage of dead branches (DB), of undersized leaves (UL), of strong (C_+) and of slight chlorosis (C_-):

$$DI = DB + (100 - DB)\,(UL + C_+ + C_-/2)\,/400$$

This decline index gives a scaled estimate of decline ranging from 0 (symptom free) to 10 (dead). Decline index values between 15 and 30 are typical of moderately damaged stands. The greatest weight for the index calculation was given to dead branches. Strong chlorosis and undersized leaves were weighted proportionally to the percentage of symptom-free branches. Slight chlorosis has a weighting of 50 % of strong chlorosis. Single environmental components, such as airborne pollutants, drought, and soil toxicity could not be differentiated from each other.

Spatial analyses and correlations to stand characteristics

Spatial autocorrelation is present, for example, when certain phenotypes tend to be associated with neighbouring individuals having a similar or dissimilar phenotype. Negative spatial autocorrelation of size, for instance, is exhibited in case small trees are predominately surrounded by large trees, or conversely, large trees are mostly surrounded by small individuals; positive autocorrelation exists if large or small trees are found in clumps. Note, that 'clumps' in this context does not entail that big or small trees are found necessarily in spatial patches related to geographical distances. Here, the term 'clump' means that for the given locations of trees – the spatial points – a non-random accumulation exists.

In this study, neighbouring points were defined from certain distance classes. For each distance class k, tree i and tree j were considered neighbours in case the distance between both trees was within the limit of the respective distance class. Eight distance classes were used: 0–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, 25–30 m, 30–35 m, 35–40 m. Thus, the spatial autocorrelation was evaluated by a specific set of paired sample trees by calculating Moran's I (cf. CLIFF & ORD 1981) that has the following definition:

$$I_k = [N \sum_i \sum_j c_{ij}\,(x_i - \bar{x})(x_j - \bar{x})]\,[\sum_i \sum_j c_{ij} \sum_i (x_i - x)^2]^{-1}$$

where I_k is the spatial autocorrelation coefficient for the kth distance class; x_i for $i = 1, \ldots, N$ is the value of the variate at each of the N points; $c_{ij} = 1$, if i j and the ith and jth tree are neighbours within the kth distance class, or $c_{ij} = 0$ otherwise; and $\bar{x}$ is the overall mean. Moran's I operates primarily like Pearson's product-moment correlation coefficient because its numerator consists of a sum of cross-products of centered values compared to the values found at all pairs of points. This spatial autocorrelation coefficient can vary between -1 and +1 for large sample sizes and has an expected value $\bar{E}(I) = -1/(N - 1)$ (CLIFF & ORD 1981). If there is complete spatial randomness in the traits represneted by x, Moran's I approaches the Gaussian distribution (SOKAL & ODEN 1978). WARTENBERG'S spatial autocorrelation analysis program (SAAP) (see LEGENDRE & FORTIN 1989 for computer program reference) was used to calculate Moran's I for all tree pairs within a given distance class, based on deviations of their respective trait from the overall mean. SAAP assesses significance of the coefficient by a resampling technique rather than by assuming normality. To detect the variation of the spatial pattern, all-directional spatial correlograms were constructed. These correlograms were tested for global significance using the Bonferroni procedure (ODEN 1984). A sample size smaller than 30 tree pairs was not

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considered. Sample sizes were therefore adequate (Daniel WARTENBERG, pers. comm. cited in WASER & MITCHELL 1990).

Spearman's rank correlation was used to investigate the relationships between spatial coefficients and descriptive stand variables. Since spatial autocorrelations of close distances provide the most useful information about the spatial pattern, correlations were performed between significant spatial measures of the first distance class (height, dbh) and forest stand variables (age, basal area, crown closure, height, tree density).

Results and Discussion

For tree height, significant autocorrelations ($p < 0.05$) were found for 57% of the sugar maple stands in at least one distance class. In total, 25% of the correlograms and 17% of the values of Moran's I were significant. The variation among different stands was high. At certain study sites, continuously decreasing spatial coefficients were estimated with increasing distance *e.g.*, stand No. 50 ($I_{0\text{-}5}$ = +0.341**, $I_{5\text{-}10}$ = +0.276***, $I_{10\text{-}15}$ = +0.208***, $I_{15\text{-}20}$ = +0.162**, $I_{20\text{-}25}$ = +0.109^{ns}), $I_{25\text{-}30}$ = –0.025^{ns}, $I_{30\text{-}35}$ = –0.235**, $I_{35\text{-}40}$ = –0.273**; $p \leq 0.01$ – **, $p \leq 0.001$ – ***, $p > 0.05^{ns}$). At other study sites, *e.g.* stand No. 102, none of the spatial coefficients for tree height exceeded ± 0.05. Fig. 2 (a) shows values of Moran's I for eight distance classes (mean over significant correlograms, mean over all significant values, grand mean) and the grand mean of expected values assuming random spatial distribution [$\bar{E}(I)$]. All three correlograms revealed positive Moran's coefficients in short distance classes and negative coefficients in longer distance classes. At certain distances, the correlograms crossed the $\bar{E}(I)$-axis. This intercept furnished a minimal estimate of the patch length and was approximately 20–25 m for tree height.

The spatial distribution of tree diameter growth was similar to the height patchiness (Fig. 2(b)). For 50% of the stands, Moran's I was significant for one or more distance classes. In total 11% of all values of Moran's I and 9% of the correlograms were significant. Spatial correlation coefficients were predominantly positive for short distance classes and negative for longer distance classes. Minimal patch size estimated (15–20 m) was slightly smaller than for tree height.

For individual decline index, the grand mean correlogram indicated a negligible, if any non-random spatial pattern (Fig. 2(c)). In total, 6% of the coefficients was significant at $p \leq 0.05$, *i.e.*, only slightly higher than the intended 5% type II error, the error committed if, as the result of the statistical test, H_o is not rejected when it is false.

No close relationships were found when values of Moran's I were rank correlated with descriptive stand characteristics (Tab. 1). A significant negative rank correlation was detected between Moran's I based on height (first distance class) and the crown closure of the stands.

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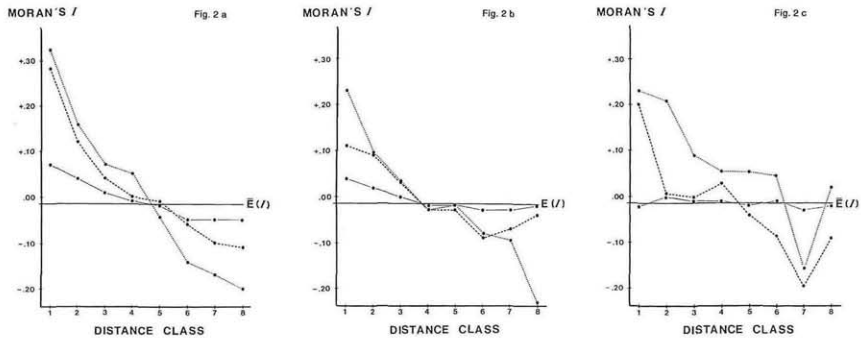

Fig. 2. Average spatial correlograms (averages of Moran's *I*-statistics for each distance class) based on significant correlograms (- - - -), significant spatial coefficients (●●●●), and grand mean (-----) for eight distance classes [0–5 m (1), 5–10 m (2), 10–15 m (3), 15–20 m (4), 20–25 m (5), 25–30 m (6), 30–35 m (7), 35–40 m (8)]: (a) tree height, (b) tree diameter at breast height (dbh), and (c) tree decline. The horizontal line on each graph indicates the grand mean of expected values assuming spatial random distribution.

The results furnish evidence for a non-random distribution of tree size (height and dbh) in space at several study sites. A similar spatial distribution pattern for the traits height and dbh was observed indicating similar patchiness for both traits. There were no significant trends between the measures of autocorrelation and stand characteristics, such as, age, basal area, height of stand, and tree density. Clumping of tree size was more pronounced in stands where crown closure was weak.

The data support the hypothesis that tree size in sugar maple is positively autocorrelated over space in stands older than 75 years. In silver maple (*Acer saccharinum*), SAKAI & ODEN 1983 detected that tree size (measured as circumference at breast height) was positively autocorrelated for distances up to 50 m. In their study, Moran's *I* exceeded 0.3 for the

Table 1.

Spearman's rank correlations of significant values of Moran's *I* of the first distance class based on height (I_H) and diameter growth at breast height (I_{dbh}) with descriptive stand characteristics (age , basal area , crown closure, stand height, stand tree density).

	Age (N)	Basal area (N)	Crown closure (N)	Stand height (N)	Tree density (N)
I_H	+0.046 (22)	–0.045 (22)	–0.523*(20)	+0.046 (22)	–0.194 (17)
I_{dbh}	+0.271 (13)	–0.325 (14)	+0.042 (13)	+0.326 (14)	–0.546 (13)

* significant at ≤ 0.05 (two-tailed test)

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first distance class (0–5 m) and decreased hyberbolically with negative values from distances of approximately 50 m upwards. In this study, many of the correlograms were not significant. But for those sugar maple stands for which spatial autocorrelations were significant, the stand structure was rather similar to that found in silver maple. However, this study has clearly shown that the spatial pattern can vary erratically among forest stands possibly due to different disturbance histories of the stands and/or anisotropy (see below).

Based on field and simulated data of diameter growth in loblolly pine (*Pinus taeda)*, REED & BURKHART 1985 have conjectured that at an early stage of a stand, all trees will be growing at their maximum rates. A positive spatial autocorrelation is to be expected. After the site is fully occupied and competition between trees is more pronounced weak trees will be eliminated. During this stage large trees are predominantly surrounded by small trees, *i.e.*, spatial autocorrelation is negative. After the stand has reached its equilibrium, formerly dominant and codominant trees will again grow approximately at the same rate. Spatial autocorrelation tends to be positive again. In this study, crown closure and tree density indicates competition or the lack of it. If REED & BURKHART's model also applies to the data of this study, crown closure and tree density should be negatively correlated with tree height and dbh. This indeed, holds true for crown closure but not for tree density. Rank correlation coefficients for Moran's *I* and tree density were negative, albeit not significant. Nevertheless, the present data support, at least in part, REED & BURKART's model.

Estimates of patch size yielded approximately 20 m based on tree height and diameter. Because correlograms intersect the *E* (*I*)-axis only once, the estimate of patch size is minimal. If the average study site had been larger, long distance values of Moran's *I* probably would have been positive again, furnishing the distance between two peaks of patches. For future investigations, the size of the study site has to be considerably larger than in this paper. For an appropriate estimation of the patch size, study site should be three or four times larger than in this study. Thus, each site should comprise approximately 300–400 trees.

To the best of the authors' knowledge, spatial distribution of environmentally damaged trees has not previously been analyzed using spatial autocorrelation analysis. This is unexpected because spatial autocorrelation has been widely used in evolutionary (*e.g.*, KNOWLES 1991) and ecological studies (*e.g.*, WASER & MITCHELL 1990, JOHNSON & LARSEN 1991).

Whereas in the past the etiology of maple dieback has often been satisfactorily explained to be due to pathological, entomological or abiotic stress (WESTING 1966), more recent damages are supposed to be caused by interacting abiotic and biotic environmental causal factors (HENDERSHOT & JONES 1989).

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The spatial patterns of declining woodland sugar maple have been visually described as being either scattered or patchy (HIBBEN 1963) and occurring seldom in clusters (WESTING 1966). Nearest-neighbour analysis was used to show that declining urban maples in Syracuse, New York occur in a non-random fashion (BURNS & MANION 1984). Trees with dead branches and necrotic leaves were distributed in a linear pattern, whereas chlorotic trees were grouped in clusters. This pattern may be related to environmental factors, such as water drainage or salt regimes. In this study, only small, if any, evidence was found that environmentally stressed sugar maple are not distributed in a random fashion. At the first glance, the mean spatial correlogram shown in Fig. 2(c) can be easily misinterpreted. It has to be recalled that with exception of the grand mean the correlograms were based on a very small number of study sites. A positive autocorrelation, *i.e.* clumping of trees with similar reaction to environmental stress was to be expected at least on a low level. In naturally regenerated maple forests, groups of consanguineous trees are present (PERRY & KNOWLES 1991) and reaction of closely related trees to environmental stress is often similar (SCHOLZ & VENNE 1989). However, the majority of the stands has been only moderately damaged and a spatial pattern might be more pronounced if the damage of the stand is more severe. It seems worthwhile to reinvestigate the stands when the average environmental damage is more distinct. Furthermore, the lack of a meaningful clumping of environmentally stressed trees is not proof that important interactive ecological forces are inoperative. Abiotic vagaries might be simply stronger that biotic interactions.

Correlograms used in this study are all-directional assuming isotropic phenomena, *i.e.* that the autocorrelation function is the same whatever direction is considered. Spatial autocorrelation coefficients produced mean values of autocorrelation irrespective of the directions. Anisotropy is often found in field data because spatial patterns of plants are frequently governed by edaphic factors (LEGENDRE & FORTIN 1989). The number of trees per study site did not allow the calculation of semi-variograms (BURROUGH 1987) or twodimensional correlograms as proposed by ODEN & SOKAL 1986. To the knowledge of the authors, tree size or tree decline have not been reported to be anisotropic. However, in an ecological study in southwestern Quebec sugar maple distribution was patchy (LEGENDRE & FORTIN 1989). When on a level among species anisotropy is realized anisotropic situation can also be presumed on a level within species. Thus, the conclusion may be drawn that anisotropy could have affected the present data analysis and have contributed to the erratic variation of spatial correlograms.

For an assessment of ecological stand stability and future stand development, information about the spatial structure within stands would be

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valuable. For instance, patches of higher or declining trees have different effects on the wind conditions than random patterns. Thus, in irregular shaped forests reflected wind gusts produce ripples in the power spectrum of the wind speed (YERG 1990) and can cause tree uprooting (SCHAETZL & al. 1989). Besides height-diameter ratio and other descriptive stand variables, measures of spatial structure could be used for an index to estimate the risk of windthrow. Although spatial autocorrelation analysis has been criticized lately (SLATKIN & ARTER 1991), this analytical tool will continue to be of considerable use in many biological areas (SOKAL & ODEN 1991).

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Recensio

SCHLEE Dieter 1992. Ökologische Biochemie. 2., überarbeitete Auflage. – Gr. 8°, 587 Seiten, 243 Abbildungen, 61 Tabellen; geb. – Gustav Fischer Verlag Jena, Stuttgart, New York. – DM 138,–. – ISBN 3-334-60393-8.

Dieses Werk enthält eine derartige Fülle von Informationen über ökologisch relevante Inhaltsstoffe, Biosynthesewege und Reaktionen bei Mikroorganismen, Pflanzen und Tieren, daß es bei dem geringen zur Verfügung stehenden Platz nicht einmal möglich ist, die Überschriften der 17 Kapitel des Buches wiederzugeben. Die Kapitel sind zu drei Teilen, „I. Organismus und Umwelt", „II. Biochemische Adaptationen an abiotische Umweltfaktoren" (u. a. Photosynthesetypen, Luftverunreinigungen als Streßfaktoren bei Pflanzen, Temperatur- und Trockenstreß, Salinität) und „III. Biochemische Wechselwirkungen im Lebensraum von Pflanzen und Tieren (Allelochemische Interaktionen der Organismen)", zusammengefaßt. Den Interessen des Rezensenten folgend, seien zu diesem dritten Teil, der 229 Seiten umfaßt, noch einige zusätzliche Hinweise gebracht. Den Anfang macht ein Abriß über Sekundärstoffwechsel und die Bedeutung der sekundären Naturstoffe. Unter biochemische Wechselwirkungen zwischen höheren Pflanzen werden Dinge wie Allelopathie (z. B. Juglon), Bodenmüdigkeit, Aspekte von Parasit-Wirt-Beziehungen bis zu Vegetationsmuster, Sukzessionen, Wurzelexsudaten und Aufnahme organischer Fremdstoffe durch Pflanzen (Abwasserreinigung!) behandelt. An biochemischen Wechselwirkungen zwischen höheren Pflanzen und Tieren werden vor allem Phänomene im Zusammenhang mit Blütenökologie (Pigmente, Düfte, Nektar, Blumenöl) und Herbivorie (Repellenzien, Attraktanzien, Cyanogenese, pflanzliche Insektizide etc.) dargestellt. Ein eigenes Kapitel gilt den Wirt-Parasit-Beziehungen zwischen höheren und niederen Pflanzen. 82 Seiten umfaßt das Kapitel über biochemische Wechselbeziehungen zwischen Tieren, das mit Farben und Biolumineszenz beginnt und bis zu den Abwehr-„Waffen" der Bombardierkäfer und anderer reicht. Den Abschluß bildet das Kapitel über Symbiosen. Das Buch ist eine reiche Fundgrube für Hinweise auf ökologische Bedeutung von chemischen Verbindungen; bei der Dichte der Information können alle Angaben natürlich nur knapp sein, wobei der chemisch Geschulte aus den zahlreichen Formelbildern zusätzliche Details entnehmen wird. Bei Bedarf nach mehr Daten ist weiterführendes Literaturstudium unerläßlich, den Weg dazu weisen – fast unglaublich – ca. 2500 Literaturzitate! Ausarbeitung des Textes und Satz sind bis ins Detail sehr sorgfältig.

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