

The Annual Rhythm of Cambial Activity in Two Woody Species of the Greek "Maquis"

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Summary

The annual rhythm of cambial activity is compared in *Arbutus unedo* and *Quercus coccifera*, two typical shrubs of the maquis in the Mediterranean-type ecosystem of Greece. The growth activity of the species is more or less focused on the favourable periods. The behaviour of *Arbutus unedo* revealed stronger correlation with moisture conditions, while that of *Quercus coccifera* seems to be more restricted in time and less controlled by moisture availability. These results indicate that both species, although growing together have different adaptive strategies to the same climatic conditions.

Introduction

Mediterranean type climate existing in 5 distinct areas of the world, all found between 32° and 40° of the Equator is a peculiar one, in which warm and dry summers alternate with mildly cold and wet winters. These oscillations induce special features on the organisms living in these areas, mostly dealing with adaptations to summer drought.

Consequently, plant species growing under this type of climate may be either evergreen sclerophylls or seasonal dimorphics concerning their survival strategy during the hot summer months (MARGARIS 1981). In this aspect it is of both theoretical and practical interest to study plant phenological behaviour, particularly considering the ever increasing use that man is making in these regions. Furthermore, this behaviour may reflect the way in which plants exploit the so-called favourable climatic periods completing their life cycles. Cambial activity is considered the best parameter in such studies because it is a process in plant development which is genetically controlled and fixed through evolution and under certain environmental limitations (AVILA et al. 1975).

This paper is a comparative study of cambial activity throughout the year in two species that grow together and are abundant in the maquis ecosystems of Greece. The species are *Arbutus unedo* (*Ericaceae*) and *Quercus coccifera* (*Fagaceae*).

Arbutus unedo is an evergreen sclerophyll species. New leaves appear during spring and some of the old mature ones have shed early in summer. Flowering occurs late in autumn and ends by the end of winter. Fruit formation and ripening process is long enough and lasts almost a year and more. The second species, *Quercus coccifera* is evergreen sclerophyll too. New leaves appear in early spring while some of the old ones fall shortly after that, in early summer. Flowering occurs during a short period in spring. Fruit formation and ripening is a long process exceeding the duration of a year (Table 1).

In the light of these data, it seemed interesting to find out whether the cambial activity of these two species has any relation with the differences in their phenological behaviour.

Materials and Methods

Branches from *Arbutus unedo* and *Quercus coccifera* growing on a "maquis" site of North Greece (Stavros-Halkidiki), were collected from January 1981 to April 1982 at one month intervals and fixed with FAA. According to FAHN (1953) and ALJARO et al. (1972) cambial activity starts simultaneously in both small branches and large stems. Therefore, the cambial activity and the localization of storage materials can be studied on stems or branches disregarding their age. For this work, 2-3 years old branches, 3-4 mm \varnothing , were used to obtain free hand sections. Toluidene blue "o" (FEDER & O'BRIEN 1968) was used to stain these sections while storage materials were localized and identified with Lugol. Sections were mounted in glycerine and observed under a Zeiss Light Microscope.

Climatic data obtained for the collection site are inserted in Table 1.

Table 1. Relation of cambial activity with climate and phenology in *Arbutus unedo* and *Quercus coccifera*

1981	Precipitation in mm	Mean monthly tempera- ture ($^{\circ}$ C)	<i>Arbutus unedo</i>		<i>Quercus coccifera</i>	
			Phenology	Cambium	Phenology	Cambium
January	27.3	2.5	full foliage flowering fruit shedding	inactive	full foliage fruit shedding	inactive
February	21.0	5.6	full foliage	inactive	full foliage flower buds fruit shedding	inactive
March	48.5	11.2	full foliage	inactive	full foliage	inactive
April	14.8	13.4	full foliage	inactive	full foliage flowering	inactive
May	12.1	17.7	new leaves partial loss of leaves fruits	inactive	new leaves partial loss of leaves	inactive
June	7.0	25.9	partial loss of leaves	inactive	partial loss of leaves	slightly active
July	6.5	25.9	partial loss of leaves	inactive	partial loss of leaves fruits	active
August	37.5	24.8	full foliage	inactive	full foliage	less active
September	0.0	22.0	full foliage	inactive	full foliage	almost inactive
October	28.0	18.3	full foliage	active	full foliage	inactive
November	65.1	7.8	full foliage flower buds	active	full foliage	inactive
December	55.0	8.2	full foliage flowering fruit shedding	less active	full foliage fruit shedding	inactive

Results

Arbutus unedo: From January to September cambial zone consists of 1—2 layers of rectangular cells. During this period there is no change of the size of the cambial zone. Signs of initiation of cambial activity are shown during October while in November this activity reaches a peak, easily demonstrated by the width of the cambial zone. In December there is a decline in the width of cambial zone, which is finally restricted to its initial size by the end of the active period (Fig. 1—9).

The annual rhythm of cambial activity seems not to be irrelevant to the amount of starch accumulated in the cells of pith and pith rays (FAHN 1958). Observations on this detail reveal that from January to March starch is hardly found in these cells. The accumulation starts from April while during June starch is abundant in pith and pith rays. This situation is continued until just before the activation of the cambial zone. It is evident that during cambial growth (October to December) storage materials are absent from both pith and pith rays (Fig. 10—18).

Quercus coccifera: Observations on this species reveal that it has shifted the period of cambial activity to warmer months, compared to *Arbutus unedo*. The month of the intense cambial activity is July, a hot dry month for the Mediterranean region. In

Figs. 1—9. Cambial activity in *Arbutus unedo* from October to December 1981. $\times 200$.

Figs. 1—3: Cambial zone before initiation of cambial activity and elimination of storage material in pith cells and rays.

Figs. 4—6: Activated cambial zone. Pith cells and rays remain free of storage materials.

Figs. 7—9: Reduced cambial activity during the last month of the year. Storage materials are still absent from both pith cells and rays.

Figs. 10—18. Inactive cambial zone in *Arbutus unedo* from April to June 1981. $\times 200$.

Figs. 10—12: Cambial activity cannot be detected while storage materials start to accumulate in both pith cells and rays.

Figs. 13—15: Accumulation of storage materials is still carried on during May.

Figs. 16—18. Accumulation of storage materials is terminated in June and leave pith cells and rays full of "energy pools". Cambial zone remains inactive.

Figs. 19—27. Cambial activity of *Quercus coccifera* from June to September 1981. $\times 200$.

Figs. 19—21: Cambial zone before initiation of cambial activity while pith cells and rays contain storage materials.

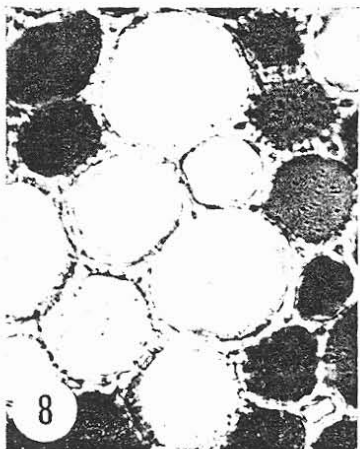
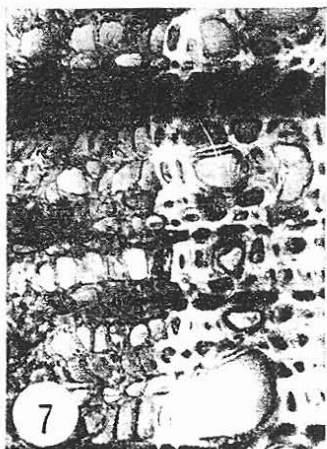
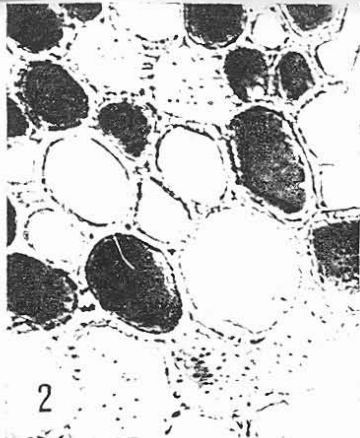
Figs. 22—24: Cambial activity is high during July. Storage materials are still visible in pith cells and rays.

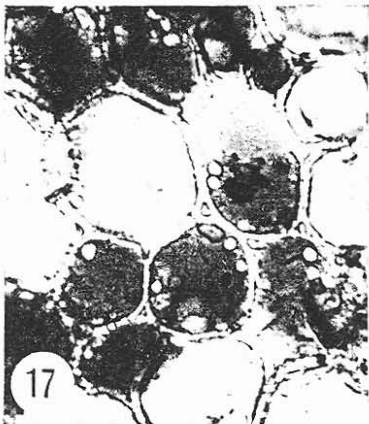
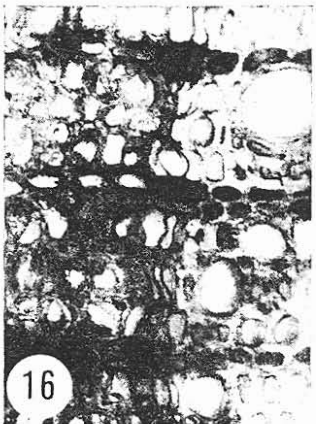
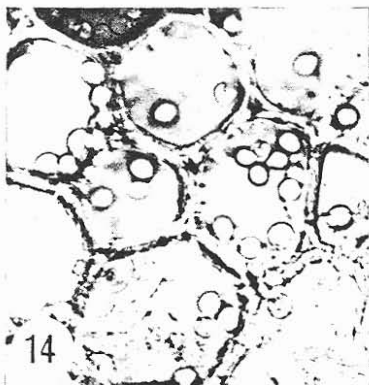
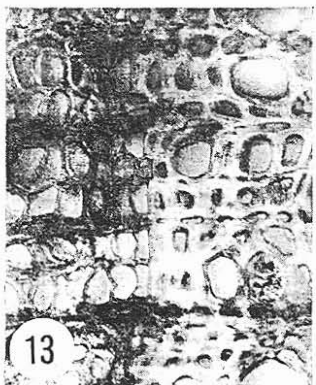
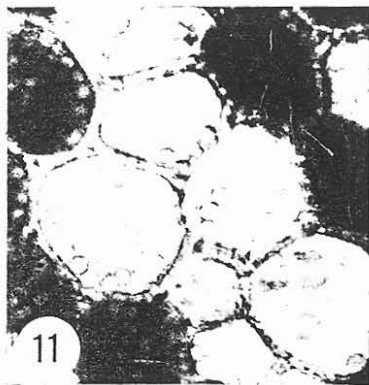
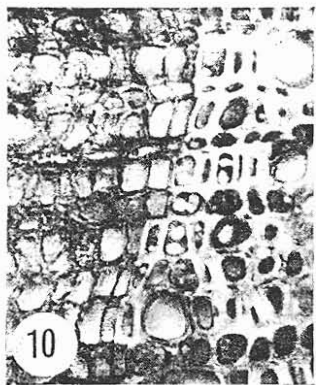
Figs. 25—27: Cambial activity is reduced while storage materials have been consumed by the end of August.

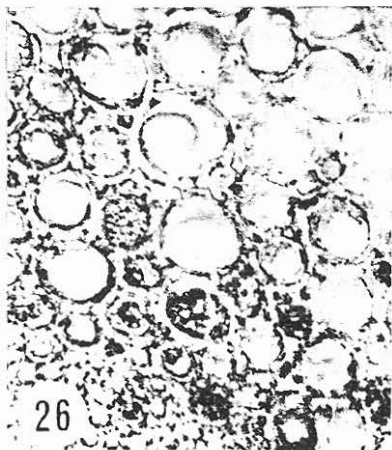
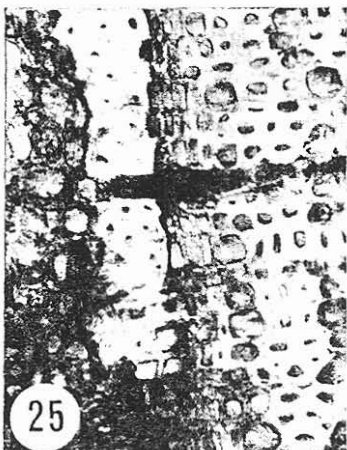
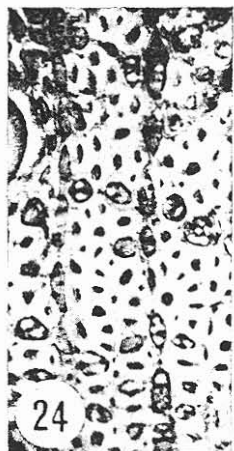
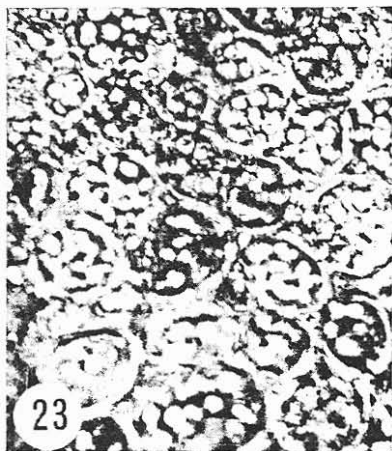
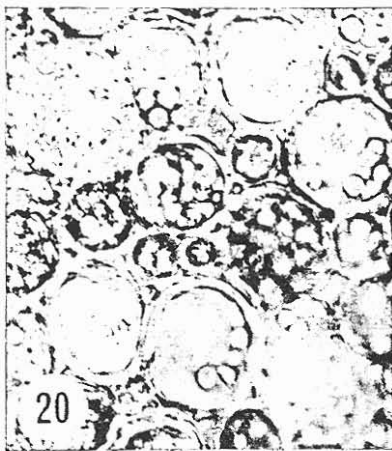
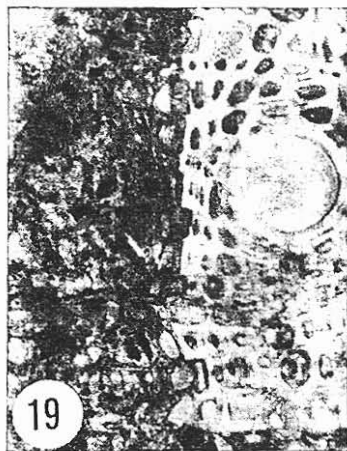
Figs. 28—36. Inactive zone in *Quercus coccifera* from January to April 1981. $\times 200$.

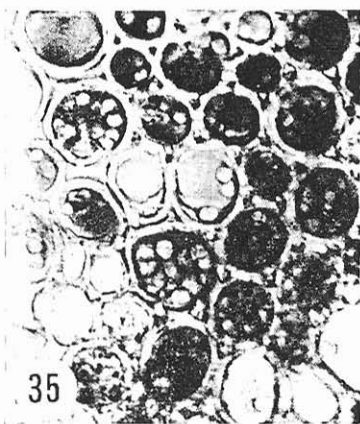
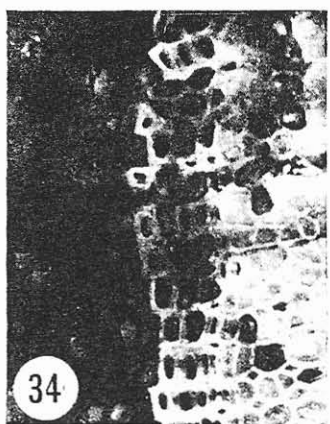
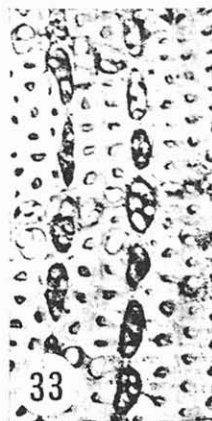
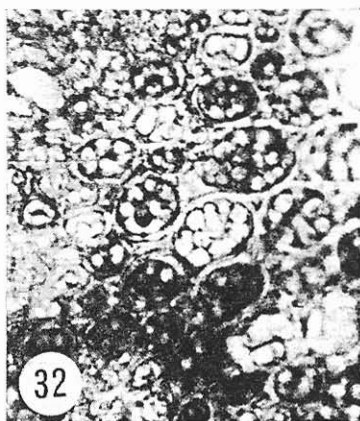
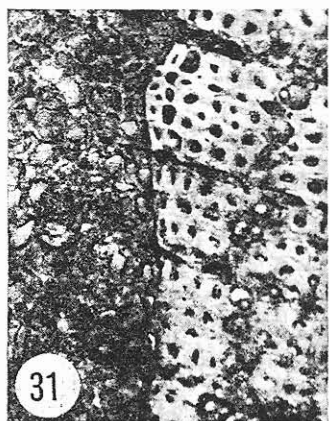
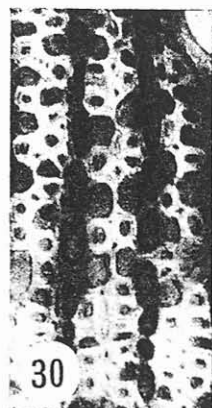
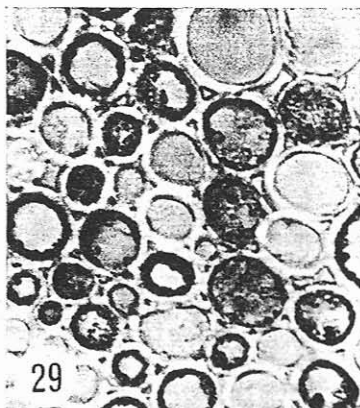
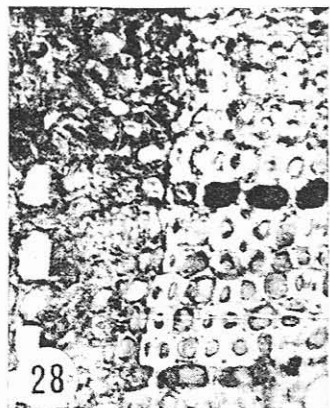
Figs. 28—30: Cambial zone remains inactive while the accumulation of storage materials has just poorly started.

Figs. 31—36: Storage materials are accumulated in large quantities in March to reach their maximum by April in both pith cells and rays. Cambial zone does not show even a slight sign of activity.









June there are signs of initiation while in August this activity stops. During the following months, particularly from February to April, cambial zone remains practically inactive (Fig. 19—27).

The annual rhythm of cambial activity correlates to starch metabolism. It is obvious that this activity starts in a period when starch is abundant in pith and pith ray cells. While cambial zone is still active starch diminishes to reach a state of complete exhaustion just by the end of the active period. Restoration of starch starts in February and seems to be completed by March when cambial zone is inactive (Fig. 28—36).

Discussion

A comparison of the annual rhythms of cambial activity in *Arbutus unedo* and *Quercus coccifera* shows that the two species behave quite differently though growing under identical climatic and soil conditions.

The behaviour of *Arbutus unedo* revealed stronger correlation with moisture conditions, while that of *Quercus coccifera* not so much. The period of cambial activity in the latter seems to be more restricted in time and less controlled by moisture availability (Table 1).

AVILA et al. (1975) comparing cambial activity in Chilean and Californian evergreen species found that in all of them appears certain activity throughout the year (even during the cold winter and the severe drought period) with maximum activity either in spring or in early summer. MARGARIS & PAPADOGIANNI (1978) found that phryganic plant species (seasonal dimorphics) appear maximum activity during spring too. Cambial activity in *Quercus coccifera* seems to fit more or less with the above, while that of *Arbutus unedo* not. The case of the latter seems to be out of the general pattern of cambial activity in the Mediterranean species studied up to now and being either evergreen sclerophylls (ALJARO et al. 1972; AVILA et al. 1975) or seasonal dimorphics (MARGARIS & PAPADOGIANNI 1978). This plant species seems to exploit the other favourable period of the year, the autumn. This observation reflects the difference in the adaptation mechanisms shown by these species though they are growing side by side.

As stated by FAHN (1958) and it has been demonstrated for other mediterranean shrubs too (MARGARIS & PAPADOGIANNI 1978), changes in starch content show a correlation with the course of cambial activity throughout the year. So, in both species studied cambial activity does not seem to be irrelevant to the consumption of storage materials. Starch is produced, accumulated and mostly consumed before the initiation of cambial activity.

In conclusion and with all necessary caution we would say that it is possible in the same ecosystem and under the same environmental conditions, for evergreen plant species to behave differently even in their basic developmental functions.

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Buchbesprechung

KINZEL, H., in Zusammenarbeit mit ALBERT, R., ERNST, W. H. O., HOHENESTER, A., KUSEL-FETZMANN, E., WEBER, M.: *Pflanzenökologie und Mineralstoffwechsel*. — Stuttgart: Eugen Ulmer, 1982. — 534 S., 178 Abb., 96 Tab., Ganzleinen, DM 148,—.

Trotz zahlreicher in den letzten Jahren erschienener Einzelpublikationen existieren kaum neuere zusammenfassende Darstellungen zur Rolle der chemischen Bodenfaktoren aus ökophysiologischer Sicht. Ausgehend von seinen langjährigen Forschungen auf diesem Gebiet unternahm daher der Herausgeber den Versuch einer Gesamtdarstellung der autökologischen Aspekte des pflanzlichen Mineralstoffwechsels. Im Mittelpunkt standen dabei Analyse und Bewertung der pflanzenphysiologischen Grundlagen, ohne daß jedoch demgegenüber der synökologische Kontext der Problematik außer acht gelassen wurde. Im Eingangskapitel wird von KINZEL zunächst das von ihm als Grundlage seiner Analysen verwendete „Physiotyp-Konzept“ erläutert, worunter die Gesamtheit der physiologischen Eigenschaften verstanden wird, die den Individuen eines Taxons gemeinsam sind. Allerdings erfolgte die Anwendung dieses Begriffs bisher nur auf Aspekte des Ionenhaushaltes.

Die einzelnen Hauptkapitel des Buches behandeln: Halophyten (ALBERT), Basenhaushalt (KINZEL), Serpentinpflanzen (KINZEL u. WEBER), Hochmoorpflanzen (KUSEL-FETZMANN), Schwermetallpflanzen (ERNST), Fluor- u. Selenpflanzen (ERNST).

Das Kapitel Halophyten bringt, ausgehend von einer Darstellung der spezifischen Ionenaufnahme bei Glykophyten und Halophyten, eine eingehende chemische Charakteristik von Halophyten natürlicher Standorte, die durch Ergebnisse von Kulturversuchen ergänzt wird. Dabei wird die unterschiedliche Strategie bestimmter Verwandtschaftskreise (z. B. Chenopodiaceae-Poaceae) zur Regulation ihres Salzhaushaltes sichtbar gemacht. Sehr umfangreich wird auf die stoffwechselphysiologischen Aspekte der Salzproblematik eingegangen, wobei erfreulicherweise für den standortinteressierten Ökologen Bezüge enthalten sind. Hinsichtlich der relativen Salzempfindlichkeit grundlegender biochemischer wie physiologischer Prozesse stimmen salzempfindliche und salztolerante Arten grundsätzlich überein. Aber nur bei den salztoleranten Vertretern gibt es die evolutiv entwickelte Fähigkeit des unterschiedlichen Einsatzes von Ionenpumpen zur Entlastung stoffwechselwichtiger Zellkompartimente. Die Behandlung der dem Halophytenkapitel angeschlossenen Gipspflanzen macht Erkenntnislücken auf diesem Gebiet deutlich. Wünschenswert wäre ein etwas ausführlicheres Eingehen auf das Problem anthropogen bedingter Bodenversalzen in ihrer Wirkung auf Glykophyten wie fakultative Halophyten gewesen.

Sehr eingehend wird der Problembereich calcicole-calcifuge (azidophile-basiphile) Pflanzen dargestellt. Erfreulich, daß der Verfasser stets bemüht ist, den konkreten Bezug zum Verhalten am Standort herzustellen und damit zur Klärung der Widersprüchlichkeit mancher der zu beobachtenden Erscheinungen beizutragen. So entsteht ein Überblick, der das Erreichte zusammenfaßt, aber auch Erkenntnislücken ausweist (z. B. die umstrittene Rolle des Nitrats für die N-Ernährung der Ericaceen).

Im Kapitel Serpentin-Pflanzen wird dargelegt, daß mehrere Ursachen für die Existenz von Pflanzen auf Serpentinböden verantwortlich sind. Dabei können Mg^{2+} -Überschuß, erhöhtes Schwermetallangebot sowie Mangel an einigen Hauptnährstoffen unterschiedlich beteiligt und Ursache des nicht selten zu beobachtenden Nanismus sein. Offensichtlich beruht dabei die Anpassung an die Existenz auf Serpentin in den einzelnen Verwandtschaftskreisen (Familien) auf unterschiedlichen Strategien.

Deutlich gemacht wird im Kapitel Hochmoorpflanzen, daß entgegen früher vertretenen Ansichten nicht ein einzelner Faktor des Komplexes Nährstoffversorgung über die Existenz der Hochmoorpflanzen entscheidet. Der Verfasser zeigt an gut ausgewählten Beispielen, daß neben mehreren „Mangelementen“ (besonders N und P) auch andere Faktoren wie Kälte und hoher Wasserstand für die Stoffproduktion jeweils entscheidende Bedeutung gewinnen können. Auch die vielfach geäußerte Vorstellung der ausschließlichen Bindung von Hochmoorpflanzen an ombrotrophe Standorte wird einer kritischen Sichtung unterzogen und an Beispielen widerlegt.

Besonderes Interesse im Kapitel Schwermetallpflanzen beansprucht die klare Herausarbeitung der zwischen Schwermetallpflanzen und Pflanzen von Normalstandorten bestehenden Gemeinsamkeiten in ihrem physiologischen Mechanismen (Aufnahme und Translokation) wie ihrer Unterschiede (Bedeutung des Grades der Schwermetalltoleranz für die Verteilung der Schwermetalle in der Zelle). Sichtbar wird auch die Bedeutung der gewählten Analytik, um auf schwermetallreichen Böden die maximal pflanzenverfügbaren Schwermetalle zu erfassen und entsprechend werten zu können.

Im Schlußkapitel wird auf die Problematik des Vorkommens auf fluor- und selenhaltigen Böden vorkommender Arten aufmerksam gemacht. Die spezifischen Mechanismen zur Tolerierung bzw. wachstumsfördernden Nutzung der genannten Elemente sind dabei zum Teil noch ungenügend bekannt.

Das vorliegende Werk kann in seiner Gesamtkonzeption wie Art der Darstellung als ein gelungener Versuch angesehen werden, den derzeitigen Stand der ökophysiologischen Kenntnisse des pflanzlichen Mineralstoffwechsels zu analysieren und zu werten. Dabei bleiben, wie vom Herausgeber selbst einleitend angemerkt, erwartungsgemäß bestimmte Wünsche offen. Eine Darstellung der Rolle des Stickstoffs im Mineralstoffhaushalt der Pflanze als eigenes, seiner Bedeutung entsprechendes Kapitel wäre sicher von vielen Seiten begrüßt worden. So finden wir zu diesem Faktorenkomplex nur verstreute, in einzelnen Kapiteln auch ausführlichere Betrachtungen, die man sich zusammengefaßt und durch andere Aspekte (N-Haushalt bei Ruderalpflanzen) ergänzt gewünscht hätte.

Letztere Bemerkungen machen deutlich, welche vielseitige Wünsche und Erwartungen sich mit dem Erscheinen eines Buches dieses Titels verbinden. Generell ist die kritische Sichtung und Aufarbeitung des dem vorliegenden Werk zugrunde liegenden umfangreichen Einzelmaterials als gelungen zu bezeichnen. Sein Erscheinen wird daher vielerorts dankbar begrüßt werden.

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