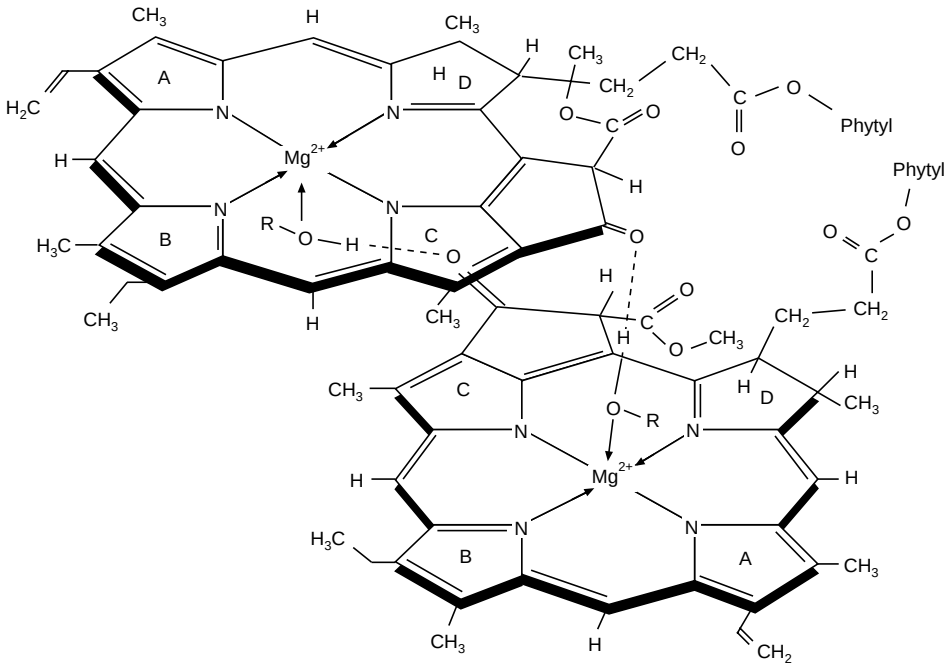
Canadian Forest Service
Forest Ecosystem Processes Network

Photosynthetic Pigments: A Bibliography



K.A. Stockburger and A.K. Mitchell

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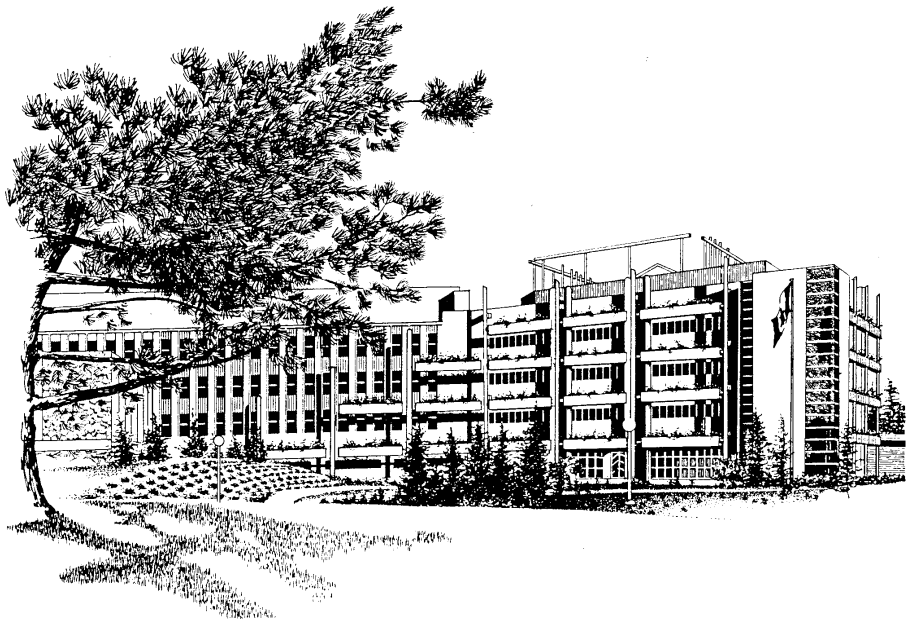

The Pacific Forestry Centre, Victoria, British Columbia

The Pacific Forestry Centre of the Canadian Forest Service undertakes research as part of a national network system responding to the needs of various forest resource managers. The results of this research are distributed in the form of scientific and technical reports and other publications.

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Forest Ecosystem Processes Network

Recent developments and advances by the forest sector in Canada have identified considerable shortfalls in the ecological knowledge base needed for sustainable forest management. This is not surprising when one considers the vastness and diversity of our forests and the complexity of forest ecosystems. However, the ability to forecast the outcomes of management decisions and natural disturbances on the composition and productivity of natural ecosystems is essential.

The Canadian Forest Service (CFS) Forest Ecosystem Process Network (FEPN) will use CFS research centres in Sault Ste. Marie, Ontario and Sainte-Foy, Quebec as lead centres, and will draw upon the talent and expertise of CFS scientists across the country. The network, in collaboration with industry, provinces, and universities, will conduct and coordinate a program of ecological research within forest ecozones of Canada. This program will focus on developing criteria and measurements for sustainable resource utilization and increase our ability to forecast how natural and man-made disturbances will shape the future forest landscape of Canada.

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Canadian Forest Service
Pacific Forestry Centre
506 West Burnside Road
Victoria, British Columbia
V8Z 1M5
Phone (250) 363-0600

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Contents

Cover illustration: Structure of chlorophyll *a* P700 of PS I (*adapted from* Goodwin and Mercer. 1983. Introduction to plant biochemistry, 2nd Ed. Pergamon Press.)

Abstract

The chlorophyll content of plant tissue is often determined as a routine analysis in ecological and physiological investigations. Carotenoids have also become useful indicators of the size and structure of the photosystems and of foliar responses to environmental change. There are several approaches to pigment analysis which include in vitro extraction and in vivo methods. This bibliography lists over 300 references related to plant pigments, predominantly between 1940 and 1998. They are arranged in five sections: photosynthetic pigments, pigment measurement, environment, physiology, and ecology. Many of the references focus on forest trees and forestry; however, some references to work on other plant species are included to give a more complete perspective. This bibliography is intended to provide readers with a guide to the conduct and application of determinations of foliar photosynthetic pigments.

Résumé

Il est souvent pratique courante de mesurer la teneur en chlorophylle des tissus, dans le cadre díétudes écologiques et physiologiques. Les caroténoïdes se sont également révélés des indicateurs utiles, lorsquíon veut déterminer la taille et la structure des photosystèmes ou examiner les réactions du feuillage aux changements du milieu. Par ailleurs, il existe plusieurs méthodes pour analyser les pigments, dont líextraction *in vitro* et les techniques *in vivo*. La présente bibliographie énumère plus de 300 publications ayant trait aux pigments végétaux, publiées principalement entre 1940 et 1998. Nous les avons classées selon cinq grands domaines†: pigments photosynthétiques; mesure des pigments; environnement; physiologie; écologie. La plupart de ces publications portent sur les arbres forestiers et líexploitation forestière, mais nous avons inclus quelques travaux ayant trait ‡ díautres végétaux, pour assurer une couverture plus complète du sujet. La bibliographie servira de guide au lecteur qui souhaite mesurer les pigments photosynthétiques du feuillage ou utiliser les résultats de telles mesures.

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Introduction

For the past 50 years, incremental improvements in chlorophyll determination have been indicative of the importance of understanding the role of foliar pigments in interpreting growth responses of plants. Determination of foliar pigments has found application in a variety of fields including plant biochemistry and physiology, crop science, horticulture and forestry. Primarily, the chlorophyll and pigment content of forest tree species has been used to address questions involving limits to photosynthesis and productivity at the branch or tree level. Of late, concerns over changes in climate and landscape-level disturbances have driven research on linking pigment analyses and remote sensing in order to derive stand and landscape-level indicators of changes in ecosystem function. Many destructive and non-destructive methods of pigment determination have been used that employ different solvents, procedures, formulas and instruments. This bibliography is intended to focus on forestry and forest trees and the history, complexity and diversity of research on foliar pigments.

History

Chlorophyll has been used as an indicator of plant health as early as 1912 and those studies mainly focused on qualitative differences at the leaf and the whole plant level. In 1913, first attempts were made to characterize foliar pigments other than chlorophyll and in the 1920's and 1930's, research focused on *in vivo* determination of chlorophyll. Some of the earliest *in vitro* chlorophyll extraction methods were explored in the late 1930s and early 1940s but these methods were cumbersome, often requiring physical separation of pigments by chromatography. In 1949, Arnon modified a procedure by MacKinney (1941) that used acetone to extract chlorophyll and employed spectrophotometry for quantitation. This method refined previous techniques and thus its use became widespread. Some researchers modified formulas by Arnon slightly and others developed equations to determine additional pigments. In the 1950s and 1960s, different methods, solvents, extinction coefficients, instruments and species were explored and the advantages and disadvantages of each were discovered.

In the 1970s and 1980s, the need to scale up from leaves and trees to stands and ecosystems has driven research on linking indicators of forest health, derived from pigment analyses, to remote sensing. Inverse relationships between chlorophyll content and leaf or fruit reflectance were shown in 1961, 1971 and 1980 using both transmission and reflectance spectroscopy. By the 1980s, hand-held instruments were developed that could be used for field studies of pigment function and attention shifted to improving the sensitivity of pigment determination and the variety of pigments that could be separated and quantified. These methods, employing reverse phase high-performance liquid chromatography (HPLC), have provided the basis for research on the interactions among foliar pigments in response to changes in environmental factors such as light, temperature and nutrition. The 1990's have seen wide spread application of these techniques in forestry.

Applications

Our interest in photosynthetic pigments and their determination arose from questions concerning growth limitations on regenerating conifers resulting from the use of silvicultural alternatives to clearcutting that employ varying levels of overstorey retention. By analyzing foliar pigment concentrations and coupling those results with other measures of foliar efficiency, including photosynthesis and chlorophyll fluorescence, we are engaged in developing physiological indicators of changes in ecosystem processes that underpin sustainability. To date, work has focused on quantifying the effects of individual environmental factors such as shade and nutrition. Future goals include developing links between foliar pigments and spectral reflectance of foliage for application in remote sensing.

The Bibliography

This bibliography lists over 300 references related to plant pigments, predominantly published between 1940 and 1998. There are a few prior to 1940 to provide a historical perspective, and there are some foreign language articles. It is divided into five main sections. The first focuses on the characterization of foliar pigments, their biosynthesis and molecular regulation. The second focuses on determination methods including extraction, and instrumentation as well as on links between chlorophyll fluorescence and spectral reflectance. The third section is oriented toward applications of pigment analyses in the development of indicators of stresses resulting from changes in environmental factors such as nutrition, temperature, and light. Physiological aspects of pigments with regards to conifers, photoinhibition and shade are presented in the fourth section. The role of pigment analysis in ecological studies and impact of pests and disease form the fifth section.

Photosynthetic Pigments

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