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Ecology of Leaf Longevity

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Cover:

Front Cover: Leaf senescence of *Fagus crenata* (Japanese beech)

Back Cover:
Left: Bud break of *Fagus crenata*
Center: Bud break and new leaf emergence of *Mallotus japonicus*
Right: Bud break of *Alnus hirsuta*

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Preface

The functional ecology of foliage is organized by seasonality. In temperate regions, leaves in deciduous forests often turn brilliant colors in autumn. In spring, buds of leaves burst and new shoots elongate. Similarly, in seasonal tropical environments species respond to the timing of rainy and dry periods, and in the aseasonal tropics subtle environmental cues can influence the timing of leafing and shoot growth. Detailed consideration reveals the diversity underlying such broad patterns of foliar phenology. Even in the canopy of a single forest, leaf dynamics are variable within and among species. Although at a glance leaves seem to simultaneously appear in spring and drop in autumn in a deciduous forest, some individual leaves in fact develop later in the season and some leaves fall during the growing season. The evergreen habit of trees can be achieved through leaves that persist over many years but is also maintained by overlapping cohorts of fairly short-lived leaves that keep the plant canopy evergreen. These complex patterns of leaf demography suggest the necessity of monitoring the dynamics of leaves per se, not merely describing the broad patterns of phenology at the tree or forest level. By monitoring individual leaves we can obtain estimates for a fundamental demographic parameter, that is, leaf longevity, and in this way move phenology from the realm of descriptive lore to that of a modern science providing quantitative and predictive understanding of plant function.

A focus on the phenology of leaves is entirely merited if for no other reason than that leaves are the most essential of photosynthetic organs. Photosynthesis is the most important chemical reaction in the world, converting radiant energy to the chemical energy that underpins life on Earth. Among the readily observed traits that characterize leaves, arguably the most broadly relevant is leaf longevity. Leaf longevity is central to leaf function and is a critical factor deciding plant fitness in a given environment. Variations in leaf longevity create a contrast between deciduous and evergreen species that define the nature of entire biomes. Leaf longevity correlates with the primary production of plant communities and gains increasing importance in relationship to global climatic change. In the past several decades, scientists have accumulated information on interspecific variation in leaf longevity for thousands of species and have produced various hypotheses and theories about leaf longevity and its consequences. This monograph is an attempt to review and synthesize our present understanding of leaf longevity.

Our own interest in leaf longevity stems from work on plant phenology that we pursued independently in the 1970s and 1980s, when the scientific study of the basis of phenological patterns was just beginning to take hold. We began our respective phenological studies on trees in the mixed-wood forests of northern Japan and eastern North America. Our interests were largely phenomenological at first, addressing questions such as why some tree species shed green leaves early in the season whereas others shed leaves only in autumn, or why some trees burst into bud earlier in spring than others. We sought explanations for these phenomena from the points of view of physiological ecology and variation in tree life history. Our thinking was drawn from phenology to more specific questions about leaf function by Brian Chabot and David Hicks' seminal 1982 review entitled "Ecology of Leaf Lifespan" and by subsequent ecophysiological work on cost–benefit analyses, especially that of Hal Mooney and Chris Field. Gradually we gravitated to deeper explanations of variation in leaf longevity rooted in the evolution of plants through natural selection under the constraints of resource availability and teamed up to organize several symposia at international meetings in ecology and botany. Our collaborations were strengthened when M.J.L. had the opportunity to spend time with K.K. in Japan, first as a guest researcher at the Hokkaido Forest Research Institute and then as a visiting professor at Kyoto University. Through those extended visits as well as shorter ones, we carried forward an exchange of ideas that laid the framework of this book.

Box 1 Evolution Through Natural Selection

Darwin

(continued)

Box 1 (continued)

In the mid-nineteenth century, Charles Darwin proposed the concept of natural selection, the foundation of modern evolutionary theory. Darwin recognized that there was some level of variation in the characteristics of individuals within a population, and that this variation in traits could affect differences in the survival and reproduction of individuals. He reasoned that over generations traits favoring greater survival and reproduction in the local environment should accumulate, or, in other words, that adaptation and fitness should increase through a process of natural selection. In Darwin's time no one knew the genetic basis of variation in traits, but now we know that the strength of natural selection depends on the heritability of traits – the degree to which characteristics can be passed from parent to offspring. Contemporary evolutionary theory combines Darwin's seminal idea of natural selection with our knowledge of genetics to explain everything from the origins of complex adaptations involving many interacting traits to the origins and interactions among species that create the diversity of life on Earth. In 1973, Theodosius Dobzhansky famously remarked that "nothing in biology makes sense except in the light of evolution."

This book considers foliar phenology through the lens of leaf longevity, which we believe can yield important insights into the functional ecology of plants. Our emphasis is on woody plants, which we know best and which also are best studied, but the principles discussed often apply as well to herbaceous species. We take pains to trace the development of ideas in the literature, partly in respect of pioneering work and also because the diverse streams of research that come together to form our contemporary view are best appreciated in historical perspective. We also purposely draw on Japanese-language publications reporting work relatively little known outside Japan. The book is intended to provide a comprehensive and coherent starting point for those just embarking on research about leaf longevity and its consequences at the levels of the whole plant, plant communities, and ecosystems.

Box 2 Phenology

Phenology is defined as the study of the timing of biological events and their relationship to seasonal climatic changes (Lieth 1974). People were conscious of the seasonal development and activity of organisms long before the scientific study of phenology emerged: survival depended on their knowing the

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Box 2 (continued)

timing of the runs of salmon up a river or the coloring of leaves as a sign of the approaching winter. In recent centuries, more precise records of phenological events began to be kept that have proven invaluable in analysis of climate change. The record of the blooming dates for cherries in Japan stretches back over 800 years and in modern times has become an integral part of meteorological reporting much appreciated by Japanese people. Based on observations of sample trees at each weather station, blooming time is predicted as an advancing front moving gradually northward as spring arrives in Japan. Similar records document the first observation of the butterfly *Pieris rapae* and the first song of the bush warbler (*Cettia diphone*), as well as observations of the timing of leaf emergence and senescence that define leaf longevity.

Phenology and Seasonality

Traditional views tie phenology to seasonality defined in terms of climatic patterns during the annual cycle defined by the planet's transit around the sun. In middle and high latitudes where there are great differences in climate throughout the year, it is certainly reasonable to expect phenological events to reflect the responses of organisms to temporal variation in abiotic constraints on their survival and reproduction. On the other hand, climatic variation at lower latitudes can be considerably less, for example, in some equatorial forests with little or no seasonal variation in precipitation, temperature, or daylength. In these situations, and perhaps more generally, we should consider that the timing of biological events may have more to do with interactions among organisms than with any abiotic factors. The timing of emergence and senescence of individual leaves in a plant can be determined as much by interactions among leaves in a growing plant canopy as by seasonal variation in climatic conditions (Kikuzawa 1995). Similarly, synchronous leaf emergence by many different species in a plant community may have been favored by natural selection, not in response to climatic constraints but because this reduced the risk of herbivory (Aide 1988, 1992). The interdependence of plants and the organisms that pollinate their flowers and disperse their fruits provides countless additional examples of this phenomenon. We should not forget that interactions within and among organisms can affect phenology quite apart from the abiotic effects of seasonal climatic change.

Box 3 Primary Production

Gross primary production (GPP) and net primary production (NPP) are terms associated with ecosystem science that characterize the capture of solar energy in photosynthesis by the primary producers in the system. The total photosynthetic assimilation of carbon by a plant community is termed gross primary production (GPP), usually expressed as ton C ha^{-1} $year^{-1}$. Some part of this assimilated carbon is used in respiration associated with growth and maintenance: the GPP minus the carbon lost to respiratory processes is termed net primary production (NPP). The annual biomass increment associated with the growth of leaves, branches, stems, roots, and reproductive structures, plus some volatile compounds and exudates, comprise NPP. Precisely estimating NPP is no easy task! Turnover of leaves and fine roots during the year, ephemeral structures such as flowers and bud scales, biomass lost to herbivores and disease, and transfers to mycorrhizal fungal symbionts all must be accounted for. At the ecosystem level, NPP can be discounted for the respiratory losses associated with the secondary production of organisms directly (herbivores, disease) or indirectly (carnivores, parasites) consuming NPP and those decomposing organic matter to obtain an estimate of net ecosystem production (NEP).

M.J.L. has enjoyed the hospitality and opportunities for intellectual growth provided by his many colleagues in Japan, but especially by K.K. This time away has been the perfect complement to the collegiality that characterizes the Department of Biology at McGill University, an academic home that could not be more congenial and stimulating. His debt is greatest, however, to his wife, friend, and colleague, Marcia Waterway, whose patient forbearance with his idiosyncrasies is exceeded only by her willingness to share her insights and ideas. M.J.L. also is grateful for enlightened and open-ended funding policies in the Discovery Grant Program at the Natural Sciences and Engineering Research Council of Canada that let him pursue research on diverse and often esoteric topics that only sometimes turn out to have practical value.

K.K. would like to express his thanks to Hiromi Kikuzawa for her encouragement and assistance in fieldwork throughout this study. Colleagues in the Hokkaido Forestry Research Institute encouraged his study for more than 20 years. Students in the Center for Ecological Research and Graduate School of Agriculture in Kyoto University and in the Laboratory of Plant Ecology in Ishikawa Prefectural University helped during his fieldwork both in Japan and in Borneo. The Ministry of Education, Science, Sports and Culture of Japan provided essential financial support.

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