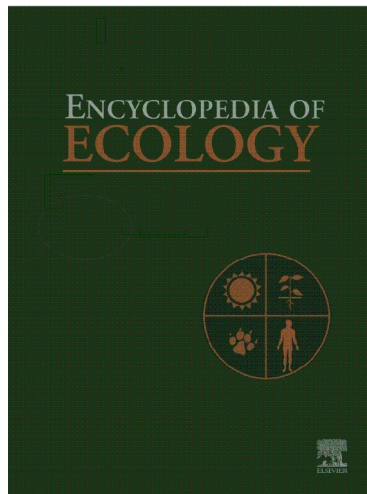


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Leaf Area Index

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Introduction

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Introduction

The plant canopy is a site of physical and biochemical processes associated with the terrestrial biosphere. The functional and structural attributes of plant canopies are dependant on species composition, microclimatic conditions, nutrient dynamics, herbivore activities, and many other activities like management. The amount of foliage in a plant canopy is one of the basic ecological characteristics reflecting the integrated effects of these factors in an ecosystem. In turn, canopy leaf area is the dominant driving force of primary production, water and nutrient use, energy exchange, and other physiological functions of a range of ecosystem processes. Understanding the organization and function of plant canopies is of central importance when conducting many types of comparative ecological studies or when developing biophysical Earth system models involving water and carbon balances. Yet, characterizing plant canopies presents many challenges, largely because of their complex geometry, and because of the difficulties of obtaining meaningful quantitative indices that relate back to fundamental processes such as light interception, transpiration, and photosynthesis. Ecophysiologicals, managers (farmers and foresters), ecologists, climate and weather forecast modelers, ecosystem modelers, and atmosphere–ecosystem interaction modelers, request information about canopy leaf area index (LAI), one of the most widely used descriptors of the canopy.

LAI is a measure of canopy foliage content commonly used in studies of vegetation and ecosystems. LAI is the total area of one side of the leaf tissue per unit area of ground surface. According to this definition, LAI is a dimensionless quantity characterizing the canopy of an ecosystem. One unit of LAI is equivalent to 10 000 m² of leaves per hectare. LAI has been recognized as the most important attribute of vegetation structure for characterizing canopies from the stand to large areas at broad spatial scales. In defining ecology as the study of the structure and function of ecosystems, LAI is one of the core parameters in ecology, as it links canopy structure and ecosystem function.

Magnitude of LAI across the World

Biomes are major biogeographic regions consisting of distinctive plant life forms (e.g., forest, grasslands, desert, etc.). LAI ranges from 1.3 ± 0.9 for deserts to 8.7 ± 4.3 for tree plantations, and up to 20 depending on the biome. Temperate evergreen forest (needle leaf and broadleaf) displays the highest average LAI (5.1–6.7) out of the natural terrestrial vegetation classes (Figure 1). Biomes with the highest LAI values are tree plantations, temperate evergreen forests, and wetlands. Exceptionally high values have been reported for hybrid poplars grown under intensive culture which could develop LAI values of 16–45, depending on the tree spacing. Those with the lowest LAI values are deserts, grasslands, and tundra.

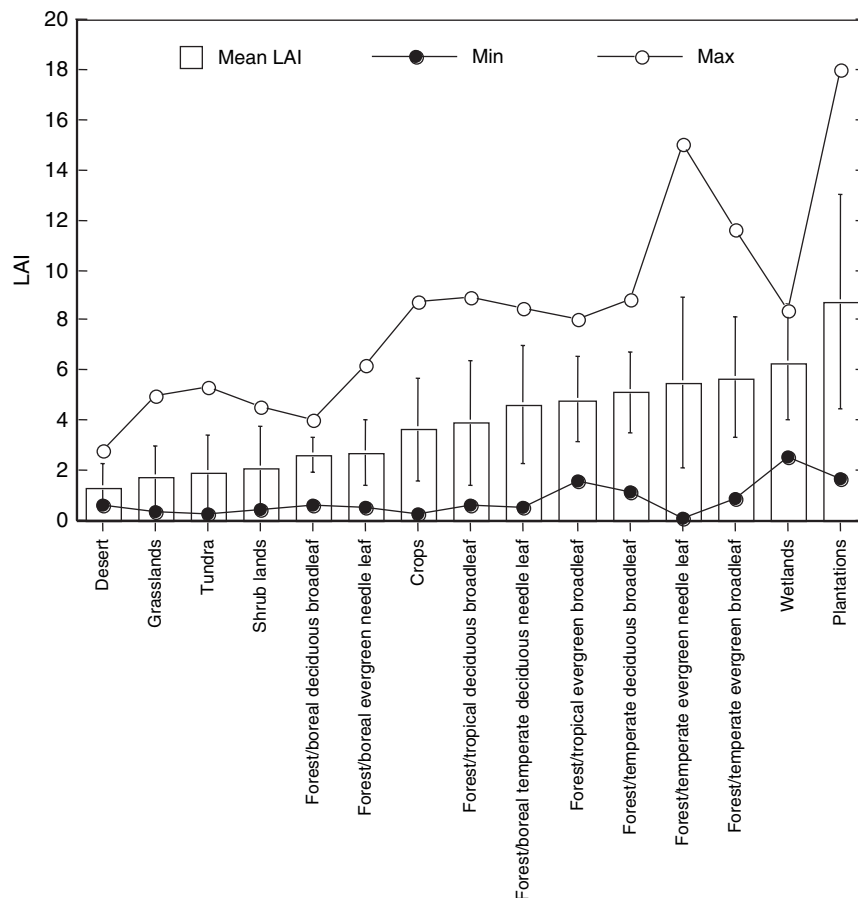


Figure 1 Mean LAI (+/- standard deviation) of biomes and cover types. Data from Scurlock J MO, Asner GP, and Gower ST (2001) *Worldwide Historical Estimates and Bibliography of Leaf Area Index, 1932–2000*. ORNL Technical Memorandum TM-2001/268. Oak Ridge, TN: Oak Ridge National Laboratory. Global Leaf Area Index Data from Field Measurements, 1932–2000. Data set available online (<http://daac.ornl.gov>) from the Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.

Environmental Controls of LAI

As climate (especially the mean and variations in annual precipitation and temperature) is the primary force shaping the major biomes of the world, much of the observed pattern of LAI distribution is initially driven by similar climatic factors. Second, biome distribution is controlled by edaphic conditions (water supply and soil fertility), which also control LAI. According to the resources optimization theory, LAI may adjust to climate and site potential. Reviews of plant science literature have computed the response of LAI to variations in soil moisture, soil fertility, and atmospheric CO₂. LAI is probably co-limited by a number of resources, including water, nitrogen, and light. A linear response of LAI to N was reported for some crops or coniferous species, but is not uniform for all plant species, soil nutrients, or fertilization rates. Fertilization (nitrogen, phosphorus, or potassium) strongly increases LAI but the response could be a short-term one, after which an acclimatization of the

canopy occurs. A new steady state is adjusted in the following growing seasons, especially in terms of leaf area versus root ratio. LAI sensitivity decreases (i.e., LAI saturates) indicating that something other than soil fertility is a limiting factor for canopy development. In many cases, water supply acts as a strong limitation resulting from LAI increase and related water uptake needs. The response to increasing soil water content is close to that of soil fertility. Increasing soil water availability in soils suffering from severe drought causes a significant increase in LAI. Interestingly, the response to increases in atmospheric CO₂ is nonlinear. LAI curves for crops and plant communities indicate a strong response of LAI to increases in atmospheric CO₂ up to the current ambient content. Afterward, the impact is more limited. At some resource thresholds, the addition of fertilizers or water will have no further influence on LAI. The saturation of LAI is likely to be indicative of light limitation, due to self-shading of leaves and negative carbon balances in low canopy layers. A large proportion of natural ecosystems

lies below a threshold of optimal resource availability. LAI saturation is a threshold beyond which any further increase in LAI is compensated for by a negative carbon balance in shaded lower canopy leaves.

Natural Temporal Variation in LAI

Both seasonal and interannual dynamics of LAI are characteristic of ecosystems, and seasonal dynamics of LAI is one of the aspects of phenology and life form. Evergreen versus broadleaved forests exhibit contrasting seasonal progression of LAI, with seasonal variation of less than 10% of LAI for evergreen. LAI expansion in deciduous species occurs within 1 month from budburst to maximum LAI which remains quite constant over the growing season and then decreases at leaf fall.

On an interannual time basis, adjusting LAI is a response of the ecosystem to cope with drought. Over a large range of climates, changes in LAI have been studied at both the individual and ecosystem scales along gradients from higher to lower rainfall amounts or from moister to drier habitats in broad- or needle-leaved tree or shrub communities. The control of LAI and morphology is often the most powerful means that a mesophytic plant has to influence its fate when subjected to long-term water stress in the field. The main response of the shrubs to different precipitation regimes in the chaparral range is to change LAI, and not physiological parameters like stomatal regulation. This adjustment is largely species dependent and both leaf size and number are affected. For example, mature eucalyptus trees are tall and produce large leaves at moist sites, whereas at drier sites, trees are shorter and tend to produce smaller leaves.

Aging of forest stands also leads to temporal changes in LAI. LAI firstly increases to a maximum at ages ranging from 16 to 50 (depending on species and site index) and subsequently stabilises or declines slightly, up to 20% lower than peak value. Interestingly, aboveground net primary production follows a similar trend with aging.

Natural canopy disturbances like fire or windstorm also induce abrupt changes in LAI. The severity of disturbance determines the regeneration options (by growth of suppressed seedlings and saplings or from the seed bank), as well as the time for stand LAI recovery. Biotic attacks by herbivores and leaf-eating insects, combined with drought, severe early spring freeze-thaw events, and fungal pathogens cause substantial reduction in LAI and hence in productivity. The loss of foliage due to insect defoliation could result in spectacular changes to LAI. Such LAI reduction could be large enough to be detected by indirect measurements, in a quantified way as compared to visual assessment of the severity of defoliation. Monitoring of LAI decrease in this way may be of importance in mapping the spatial extension of the attack, may help to predict stand

dieback and eventually plant mortality in the following years. Whatever the kind of natural disturbance or extreme event, the time needed to recover pre-event LAI could be used as an index of ecosystem resilience.

Management of LAI

Except in natural ecosystems, the canopy is periodically managed by farmers, foresters, grazing animals, and agriculturists. All management operations including cutting, grazing pasture, thinning, fertilization, liming, mowing, pruning, species sawing, and high herbage use, affect LAI. As stocking rate increases in grazed pasture, the total consumption per hectare goes up, while the net primary productivity decreases. The LAI is usually 2–3 with lower stocking densities and 1–2 at higher densities. In both crops and young forests, fertilizer effects on LAI are significant, and should increase LAI up to 3 units. An example of LAI management in forests is thinning, which reduces stand basal area, density, and LAI. In some cases, especially in even-aged mono-species stands like coniferous plantations, the LAI reduction is proportional to the basal area removed. Nevertheless, in most cases, the percentage of basal area removed is not proportional to those of LAI. Thinning improves water balance, radiation penetration within the canopy of the remaining trees, soil biology, and organic matter mineralization as a result of microclimatic changes. Canopy recovery occurs over several years depending on the intensity of the thinning, tree age, and site fertility (Figure 2).

Managers control LAI to control productivity and water uptake, but in fact agricultural and forest managers should be interested in using estimates of LAI to gauge the vigor of cultures or plantations (crop or forest decline, pathogen attacks), to adjust management practices and thus produce optimum LAI (Figure 3).

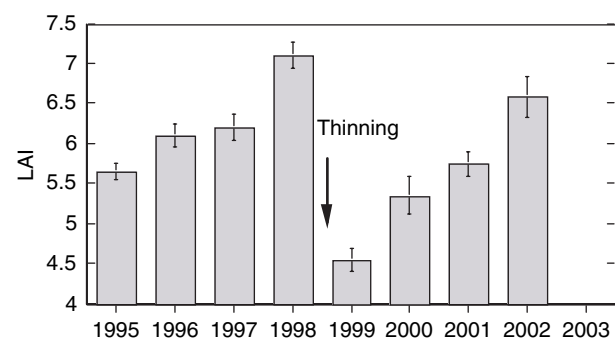


Figure 2 Stand LAI recovery after thinning in a beech stand (RENECOFOR Network, Plot HET88). LAI was measured using a plant canopy analyzer (LAI 2000, Li-Cor, Nebraska, USA). Data from N. Bréda.

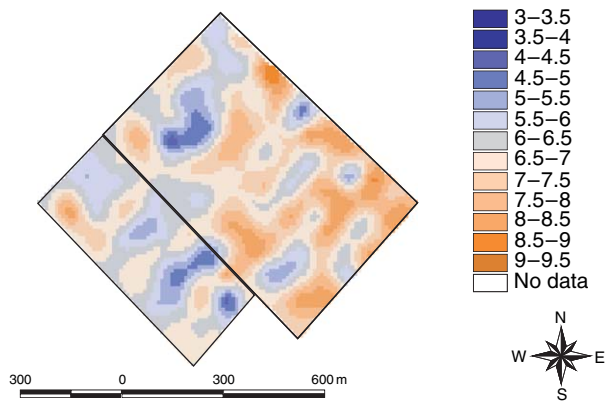


Figure 3 Spatial variability of LAI in 60 ha of a managed beech forest (Hesse, France). Ground-based LAI measurements were distributed according to a systematic network (50 m x 50 m) using two cross-calibrated plant canopy analysers (LAI 2000, Li-Cor, Nebraska, USA). The scale ranges from 2 to 6, i.e., a similar range to that of the biomes presented in **Figure 1**. Variations in LAI are due to stand age, date, and intensity of last thinning, soil properties, and species composition. For further details, see Bouriaud O, Soudani K, and Bréda N (2003) Leaf area index from litter collection: Impact of specific leaf area variability within a beech stand. *Canadian Journal of Remote Sensing* 29: 371–380.

LAI as a Descriptor of Canopy Structure

Canopy structure means: (1) the whole of the vegetation community including species, number, leaf area, and leaf history; (2) its spatial organization, horizontal and vertical arrangement; and (3) its time progression (season, year, decade, and more). Then geometric complexities of different canopies are reduced to a simple quantification of the sum of all leaf layers as LAI.

The vertical distribution of LAI in mixed canopies reflects the functional abilities of species or leaves (shade, air humidity, and temperature tolerance). LAI controls both within- and below-canopy microclimate, determines and controls rainfall, snow and deposition interception, radiation extinction, wind velocity slackening, light quality and quantity below the canopy, and hence influences the living conditions of fungi, plants, insects, macro- and micro-fauna communities.

LAI as the Driving Force of Canopy Exchanges

LAI describes a fundamental property of the plant canopy in its interaction with the atmosphere, especially concerning radiation, energy, momentum, and gas exchange. Stand function includes: (1) the rate of biological energy flux through the ecosystem, that is, rates of production and respiration; (2) the rate of material and nutrient cycling, that is, the biogeochemical cycles; and

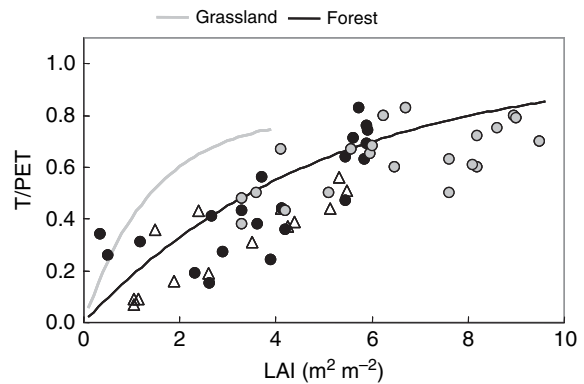


Figure 4 Transpiration ratio (T/PET) as a function of LAI for forest and grasslands. For forest, symbols are for phenological periods: triangles: LAI increase during leaf expansion; black circles: LAI decrease during autumn; gray circles: maximum LAI for contrasting stands. Data from Granier A, Bréda N, Biron P, and Villette S (1999) A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* 116: 269–283 and Saugier B (1996) Evapotranspiration des prairies et des cultures. *Comptes-rendus de l'Académie d'Agriculture de France* 82: 133–153, for forests and grasslands, respectively.

(3) biological and ecological regulation, including prevention of soil erosion and regulation of water uptake, or radiation interception and conversion. LAI is the favored canopy variable because it is required for estimating many process rates, from canopy gas exchange to nutrient return in litterfall, including understory microclimate control and competition for light, water, and mineral nutrients.

LAI acts as the canopy–atmosphere interface where water and carbon gas exchange occurs and is, therefore, a core parameter of biogeochemical cycles in ecosystems. Any change in canopy LAI, as a result of frost, storm, defoliation, grazing, drought, or management practice, is accompanied by modifications in stand productivity. Process-based ecosystem simulations require LAI as a key input parameter to produce quantitative analyses of productivity. When LAI of a community is low (<4), which is usually in arid environments or during the establishment of a crop, the transpiration rate (T/PET) is linearly related to LAI. Beyond this point, transpiration rate increases more slowly due to: (1) the saturation of canopy radiation interception and (2) soil water availability limitation (**Figure 4**). Growth rates are also dependent on LAI, but as LAI increases, the growth rate reaches a maximum value. Thereafter, it may decline. The existence of an optimum LAI was first observed for herbaceous plants. At the slope inflexion, called critical LAI, an increase in LAI and its associated CO_2 uptake will not counterbalance the reduction of CO_2 uptake in the existing leaf area because of self-shading. The community might still continue to gain in biomass, but at a lower

rate. Plant growth and life form strongly affects optimum LAI depending on leaf angle, clustering, and vertical distribution of leaves resulting in differences in the self-shading and greater or lesser depths of penetration of light into the canopy.

Assessment of LAI

Despite its functional importance, the measurement of LAI is not easy, due to its spatial (horizontal and vertical) and temporal heterogeneity. A plethora of ground-based optical, allometric, or litter collection methods and remote sensing approaches to estimate LAI are available.

Direct or Semidirect Methods

These involve a leaf area measurement. The main advantage of direct methods is that they are the only ones giving real LAI without any other plant organs. For that reason, they are considered as reference methods for indirect and remote sensing calibration. However, these direct methods are tedious, time consuming, and some of them are destructive.

Harvesting

The harvest method is one of the oldest methods, used for various vegetation types from crops to forests. A sample to be treated destructively has to be collected 4–5 times during the crop life cycle (i.e., sampling is done at 10–15 day intervals from seedling emergence) or relative to some of the developmental stages of the crop (emergence, flowering, physiological maturity). At each collection date, leaves are separated from the other parts and subsamples are selected for leaf area measurements. Then leaf area models have to be calibrated as: leaf area = (leaf length \times leaf breadth) $\times k$, where k is a species specific coefficient depending on leaf shape and indentation ($k=0.5$ for triangle, 0.75 for grasses such as sorghum and maize, near 2/3 for many dicots). Leaves of the subsample are dried, weighed, and the dry leaf weight ratio is computed. Finally, LAI is computed as the dry weight of leaves \times dry leaf weight ratio.

Litter collection

Using traps, in nets, or sampled on the ground is useful for LAI calculation of broadleaved plants. Species composition in the canopy is not distinguished when using canopy LAI. By sorting leaves from different species in mixed broadleaved forest, the contribution of each species from the community may be quantified (Figure 5). Few data exist on leaf biomass of temperate deciduous forest communities which include undergrowth. If biomass is nearly negligible as compared to total stand biomass, the

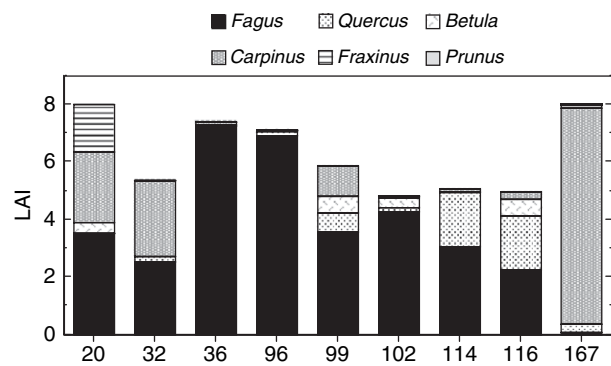


Figure 5 Species contribution to total stand LAI in beech-dominated forest as estimated by litter collection and species sorting. Each plot number is related to spatial variability within the stand. For further details, see Bouriaud O, Soudani K, and Bréda N (2003) Leaf area index from litter collection: Impact of specific leaf area variability within a beech stand. *Canadian Journal of Remote Sensing* 29: 371–380.

contribution of leaf area of undergrowth has been demonstrated to be a significant part (from 15% to 60%) of LAI of the whole community (tree or shrub layer + ground vegetation) within a narrow range of 7. Finally, the measured leaf properties (individual leaf area, specific leaf area, number of leaves, etc.) are of key importance for a comprehensive analysis of LAI changes between stands, species, or dates. Indeed, differences in LAI for a given stand during certain years could be the result of any change in number of plants, number of leaves, or individual leaf area.

Allometry

A relationship exists between sapwood or tree basal area and leaf area. This destructive approach is site-, species-, age-, and management dependent. Allometric relationships give the state at a given date.

Indirect Methods

These use the consequences of LAI on radiation interception or reflectance and are nondestructive. As any measure of radiation, these methods are sensitive to sky condition (direct vs. diffuse radiation or a clear and stable sky).

Ground-based approaches using optical instruments

At plot or stand level, the most common method of estimating LAI and its seasonal variation is from measurements of the fraction of light transmitted through the canopy to the ground. Nondestructive optical methods have been developed to estimate LAI periodically. The simplest approach, using Beer's law inversion with an extinction coefficient depending on the crop or tree

properties, is useful and efficient for crops and broad-leaved forests. However, for many evergreen species, the procedure requires some corrections to take the clumping of needles and branches into account. In any case, accurate equipment and methods for ground estimates of LAI are now available. Optical methods of estimating LAI use the inversion of gap fraction data. One fruitful approach involves measurement of the gap fraction, the proportion of unobscured sky in a set of sky directions as seen from beneath a plant canopy. Recent advances in the theory make it possible to calculate a useful array of canopy properties from gap fraction measurements, including light extinction coefficients, LAI, and leaf angle distribution. A variety of techniques can be employed to obtain gap fraction measurements, such as linear arrays of light sensors (SunSCAN, Delta-T Devices Ltd., Cambridge, UK and AccuPAR, Decagon Devices, Pullman, USA). Two other devices measure gap fraction for different zenith angles. The LAI-2000 (Li-Cor, Lincoln, Nebraska, USA) measures 5 zenith angles simultaneously, through a fisheye light sensor, while the DEMON instrument (CSIRO, Canberra, Australia) measures direct beam radiation from the Sun through a directional narrow angle of view (0.302 sr). Measurements with the DEMON instrument have to be repeated several times from early morning until noon to collect data over a range of zenith angles. Hemispherical photography and imaging hemispherical sensors (e.g., the CI-100 Canopy Analyzer, CID, Vancouver, USA) are also widely used but these frequently underestimate LAI.

Remote-sensed approaches

As opposed to ground-based methods, remote sensing deciphers the reflected, instead of the transmitted radiation. The plant communities are full of chlorophylls, a set of pigments which absorb part of the solar radiation for photosynthesis. As a result, reflectance of radiation in different spectral bands, especially the two widely used infrared and red ones, is changed proportionally to the amount of green vegetation. Since large-area maps of LAI are needed for global land-surface modeling, plenty of empirical relationships (i.e., statistical correlations) have been proposed between satellite or airborne image reflectance and ground-based (*in situ*) estimations of LAI. There are many vegetation indices developed from radiances in a wide range of channels corresponding to spectral bands. LAI estimation from satellite data requires ground data for validation and testing for bias. Satellite data must be corrected for atmospheric effects, thus requiring additional information on the state of the atmosphere (especially water vapor, aerosols, and ozone). Nondestructive (optical) measurements are the preferred approach for obtaining ground measurements. Classical values of LAI derivation from remote sensed vegetation indices (like Normalized Difference Vegetation Index,

NDVI) range from 0 to 4–5, fitting an empirical exponential function with a plateau indicating a saturated signal for higher LAI. Such a relationship was first established for wheat and maize, at various states of growth. Unfortunately, LAI often reaches values above 5 and up to 15 in temperate mixed broadleaved forests or coniferous plantations. Then remote LAI derivation is not well adapted for such kinds of vegetation. New algorithms using the intrapixel variability of signals have been proposed but remain to be tested using ground-based data sets of forest LAI differing from the calibration data set.

Worldwide Maps of LAI and Controversies About Scaling in Global Modeling

Because LAI is a dimensionless quantity and an extensive surface parameter, it can be measured, analyzed, and modeled across a range of spatial scales, from individual tree crowns to whole regions or continents. Estimation of LAI across a landscape is needed for regional ecosystem analysis or modeling, but recent meta-analysis of worldwide LAI measurements highlights weaknesses in the ecological and geographical coverage of LAI measurements on a global basis. LAI is a canopy parameter in several models of growth or net primary production, but also in interactive models of land surface and atmospheric processes. Across wide landscapes, remote sensing is used to derive LAI maps to initiate regional or global modeling and automatic mapping of LAI at 8 km spatial resolution (NASA MODIS satellite data) offers global coverage of the biosphere. The reason for such a broad global ecological research interest in LAI is due to its emergent properties but it is still the subject of controversy in terms of scaling.

See also: Biomass, Gross Production, and Net Production; Ecosystems; Evapotranspiration; Forest Models; Leaf Area Index Models; Life Forms, Plants; Light Extinction; Plant Ecology; Remote Sensing; Seasonality; Tree Growth; Water Cycle Management.

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Relevant Website

<http://daac.ornl.gov> – DAAC-Distributed Active Archive Centre, for biogeochemical dynamics, Oak Ridge National Laboratory.

Learning

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Introduction

What Learning Is

Who Learns

Why Learn

Learning in an Ecological Context

Learning and Evolutionary Change

Learning and Species Interactions

Further Reading

Introduction

Learning is ubiquitous among animals and plays an important role in all manner of ecological processes including competition, predation, mutualism, species coexistence, and population regulation. Learning has important consequences for evolutionary change, including biological diversification. Learning is also important to consider when assessing the effect of human activity on animal populations. Here we provide an overview of learning from an ecological and evolutionary perspective.

What Learning Is

The definition of learning has been the subject of long, unresolved debate, and no definition is universally accepted. However, most students of animal learning agree that learning involves a repeatable change in behavior with experience that persists for some time after experience ends (i.e., there is evidence of memory). Furthermore, with a few important exceptions, learned behavior changes gradually with continued experience to

some asymptote; wanes if not continually reinforced; can often be undone by a new type of experience; and is more suited to the environment in some way (i.e., associated with higher fitness) than before learning took place.

Learning is just one form of behavioral plasticity. Learning is sometimes referred to as a form of phenotypic plasticity in which the phenotype is behavior. This is not imprecise, but can be somewhat misleading because behavior is itself a form of phenotypic plasticity. Behavior, like any form of phenotypic plasticity, can be described by a 'reaction norm' that relates an animal's phenotype, in this case a set of morphologies generated by motor outputs, to particular environmental states. Learning in turn can be described as a mechanism by which the reaction norm representing a particular behavior is modified by experience with the environment. Learning is thus a mechanism of plasticity in behavior, which is itself a type of plasticity.

While learning is an important mechanism of behavioral plasticity, behavioral plasticity also results from motivational and maturation processes. For example, females from a given butterfly population may respond to the same host plant cue in different ways (e.g., laying eggs or not), depending on the number of eggs that are currently matured. The more number of eggs that are matured, the