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ORIGINAL PAPER

Wetlands as energy-dissipating systems

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Abstract Since wetlands are ecosystems that have an ample supply of water, they play an important role in the energy budgets of their respective landscapes due to their capacity to shift energy fluxes in favor of latent heat. Rates of evapotranspiration in wetlands are commonly as high as 6–15 mm day^{-1}, testifying to the large amount of energy that is dissipated through this process. Emergent or semi-emergent wetland macrophytes substantially influence the solar energy distribution due to their high capacity for transpiration. Wetland ecosystems in eutrophic habitats show a high primary production of biomass because of the highly efficient use of solar energy in photosynthesis. In wetlands associated with the slow decomposition of dead organic matter, such as oligotrophic marshes or fens and bogs, the accumulation of biomass is also high, in spite of the rather low primary production of biomass. Most of the energy exchange in water-saturated wetlands is, however, linked with heat balance, whereby the largest proportion of the incoming energy is dissipated during the process of evapotranspiration. An example is shown of energy fluxes during the course of a day in the wetland ecosystem of Mokré Louky (Wet Meadows) near Třeboň. The negative consequences of the loss of wetlands for the local and regional climate are discussed.

Keywords Wetlands · Vegetation · Energy fluxes · Primary production · Landscape management

Introduction

The Sun, which may be considered an absolutely black body with an approximate temperature of 5,900 K, emits radiation that peaks in intensity in the visible region (400–700 nm; this also includes most of the radiation that is used in photosynthesis). Solar radiation is greatly diminished in intensity as it passes through the Earth's atmosphere, and its spectral composition is modified. Figure 1 shows the spectra of an absolutely black body with the Sun's temperature, solar radiation reaching the upper boundary of our atmosphere, and solar radiation reaching the Earth's surface after passing through the atmosphere.

The solar radiation incident on a plant stand is partially reflected (albedo), but most of it penetrates into the stand (net radiation). In plant stands, the net radiation is used as an energy source to evaporate water from the plants plus soil (evapotranspiration), or it is transformed into sensible heat. A small proportion of the radiant energy is used to warm the plants and soil. Only 1–2% of the net radiation is usually utilized in the process of photosynthesis (Fig. 2). The sum of the sensible heat (heat that manifests itself as a temperature increase) and the latent heat used for evapotranspiration can represent more than 90% of the net radiation.

Wetlands are ecosystems that are permanently or at least temporarily amply supplied with water, which has a

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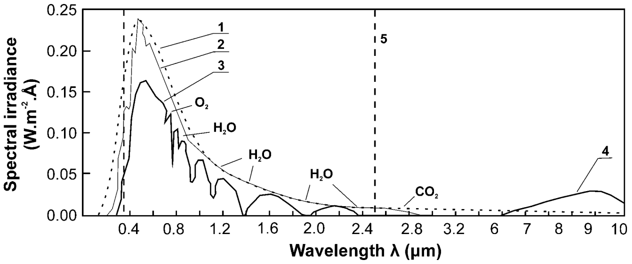


Fig. 1 Spectral changes in solar radiation caused by its passage through the atmosphere. The three main atmospheric gases (O_2, H_2O and CO_2) significantly influence the spectrum of the incident light (according to Rosenberg [17]). The *numbers* indicate the following spectral lines: *1* radiation intensity of a black body with the approximate temperature of the Sun ($T = 5{,}900$ K according to Planck's law); *2* solar radiation incident on the atmosphere; *3* solar radiation incident on the Earth's surface at sea level; *4* radiation emitted by the Earth's surface ($T = 300$ K according to Planck's law); *5* spectral permeability of glass. Wavelengths of less than 2.5 μm pass through glass

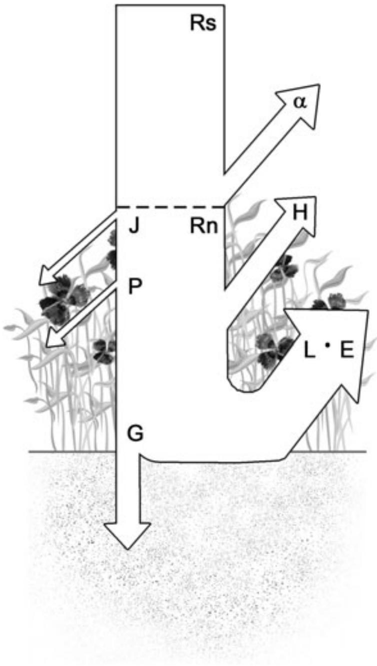


Fig. 2 Distribution of the solar energy incident on vegetation. R_S global radiation, *Rn* net radiation, α reflectance (albedo), *H* sensible heat flux, $L \cdot E$ latent heat flux, *G* ground heat flux, *J* accumulation of heat in biomass, *P* photosynthesis, $Rn = H + L \cdot E + G + J + P$

profound influence on their energy budgets. Wetland plant stands with their canopies above the water surface are the main actors in energy transformations leading to energy dissipation in wetlands. As a rule, a substantial proportion of the incoming solar radiation is thus used for evapotranspiration.

The aim of this paper is to describe the specific features of the energy fluxes and transformations that make wetland ecosystems highly effective at energy dissipation. Some attention is also paid to the methods used to study these processes.

This is very much in line with Professor Ivan Málek's emphasis of the functional approach to ecology, which he and his collaborators pioneered during the International Biological Programme (IBP, 1965–1974). Within this programme, Ivan Málek served as convenor of the Production Processes (PP) section, which concentrated mainly on the mechanisms and relationships that drive plant photosynthetic production and biological nitrogen fixation. In 1969–1974 he was also Vice-President of the Scientific Committee for the entire IBP (SCIBP), and therefore earned great credit for the success of the IBP. Within his own country, he served as chairman of the Czechoslovak IBP National Committee in 1965–1970, and thus managed to mobilize a great number of Czechoslovak scientists around the IBP in the service of a process-oriented ecology. In this context, he also supported the foundation of the IBP Wetlands Working Group by Czechoslovak, Polish and Romanian scientists in 1970. This working group still continues its activities under the umbrella of the International Association for Ecology (INTECOL).

Specific features of energy fluxes in wetland ecosystems: primary production and decomposition of organic matter

Wetlands which are eutrophic, i.e., well supplied with plant mineral nutrients, are highly productive because they do not suffer from water shortage as a rule. Individual types of wetlands differ significantly not only in their production of plant biomass, but also in their capacity for the long-term accumulation of dead organic matter (as detritus or peat). This capacity depends on the ratio between the average rates of primary production and decomposition. For example, bogs are distinguished by a low annual primary production of biomass (usually only 100–250 g m^{-2} of dry mass). Nonetheless, the strongly suppressed decomposition of organic matter produced in bogs results in a net annual accumulation of dead plant biomass which is eventually transformed into peat. In contrast, eutrophic fishponds, where the primary production is one order of magnitude higher than in bogs, often accumulate hardly any dead biomass because the annual decomposition approaches or equals the annual net primary production. In fishponds, however, as in other wetlands, the production:decomposition ratio depends on the nutrient (especially P and N) supply, i.e., on the trophic status of the water. Biomass (both live and dead) accumulation implies the accumulation of energy fixed by photosynthesis, whereas intense decomposition results in the dissipation of this energy and the reduced sequestration of CO_2 from the atmosphere and water.

The most valuable and largest sets of data on primary production in wetlands were obtained during the IBP, with a substantial contribution from Czechoslovak scientists [4, 5, 7, 19]. Another rich source of data on primary production by wetland plants is the handbook by Hejný and Sytnik [8]. Figure 3 shows data on seasonal production by various types of wetland plants [4, 19]. In stands of natural wetland vegetation growing under optimum conditions in the temperate zones, a reasonable estimate of the average annual dry matter production per unit area of the ground is 1 kg m^{-2}. The average daily rate of plant dry matter production is as much as 10 g m^{-2} day^{-1}, which corresponds to a daily average energy flow of about 4 W m^{-2}. The photosynthetic rate, expressed in energy terms, then attains values of several W m^{-2}.

The rate of decomposition of dead organic matter (litter or detritus), as carried out predominantly by microorganisms and fungi and expressed in energy terms, can be several times as high as the rate of production and accumulation of organic matter during the process of primary production, i.e., several to tens of W m^{-2}.

Using the energy content in the biomass produced and that in the radiation intercepted by a plant stand over the same time period, we can estimate the net efficiency of the conversion of solar energy into the energy contained in plant biomass. During the process of photosynthesis, the efficiency of solar energy conversion decreases with each successive step of photosynthesis (for more details see, e.g., Blankenship [1]), so that the final net efficiency is usually between one and a few percent of the incident global radiation, and about twice as much of the incident photosynthetically active radiation (380–720 nm). Petr et al. [12] report on the net efficiency of solar energy conversion for the production of four grass species, among them the wetland grasses *Phalaris arundinacea* L. and *Glyceria maxima* (Hartman) Holmberg, for which the efficiency was 3.3% across the whole growing season.

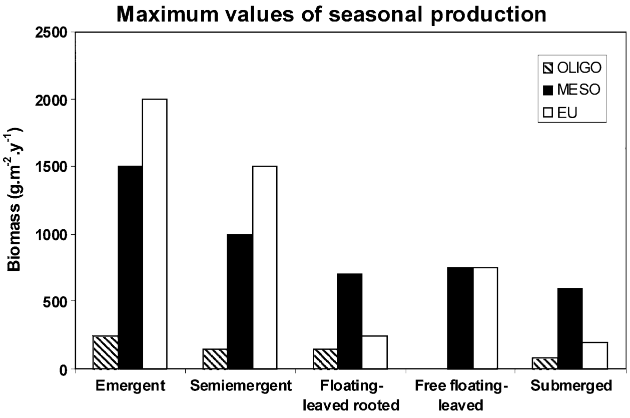


Fig. 3 Maximum values of seasonal production. Common values for the seasonal production of biomass attained by temperate-zone aquatic and wetland macrophytes [4, 19] in oligotrophic (*OLIGO*), mesotrophic (*MESO*) and eutrophic (*EU*) environments are shown (after Květ et al. [10]). Emergent macrophytes only have photosynthetically active leaves above the water's surface (e.g., *Phragmites*). Semi-emergent ones have leaves above, on and below the water's surface (e.g., *Saggittaria*)

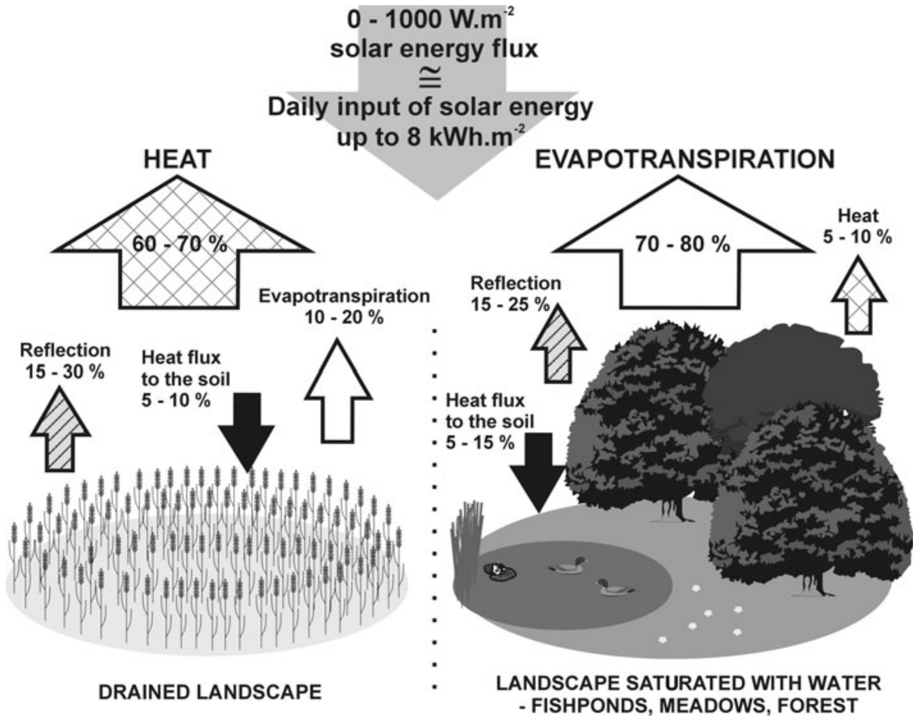
Specific features of energy fluxes in wetland ecosystems: evapotranspiration and heat balance

Although photosynthesis is essential for the existence of life on Earth, it plays only a minor role in the transformations and dissipation of the energy of the incident solar radiation. Much greater amounts of the incident solar energy are used by plants for transpiration. Evapotranspiration, which is the sum of transpiration and evaporation from the vegetated soil or water surface area, is a highly dynamic process that depends on the energy input and the amount of water available to the plants. The overall energy distribution in an ecosystem therefore greatly depends on its management. In ecosystems with an ample water supply—such as wetlands—most of the energy input is transformed into latent heat of evaporation, whereas on dry sites (e.g., sites that have been drained or are lacking in vegetation) it is converted into sensible heat, significantly increasing the local temperature (Fig. 4).

Evapotranspiration may consume 400 W m^{-2} or more. If we compare a wetland area and a dry area, the difference in the distribution of solar energy between the latent heat of evaporation and sensible heat amounts to several hundreds of W m^{-2} on a sunny summer day. Evapotranspiration has a dual air-conditioning effect—it cools evaporating sites with excessive energy input, and warms up cool sites, where the water vapor condenses. The ground heat flux is usually several to tens of W m^{-2}. It is directly proportional to the soil moisture content. On sunny days, a concrete surface reflects as much as 200 W m^{-2} (albedo $\sim$23%), while the surface of a lake does not reflect more than 50 W m^{-2} (albedo $\sim$6%). Reflectance does not differ much between different vegetation types, and is around 150 W m^{-2} (albedo $\sim$17%). For most of the year, less radiation is reflected by vegetation that is well supplied with water.

The ratio between the energy of the solar radiation transformed into sensible heat and that used for evapotranspiration is called the Bowen ratio [2]. In wetland plant stands, where most of the radiant energy is transformed into latent heat of water evaporation (2.45 MJ = 0.68 kWh per 1 L of water at 20°C; [6]), the Bowen ratio is usually smaller than 1. The same amount of energy is released during the process of water vapor condensation.

Fig. 4 Distribution of solar energy in a drained landscape and in a landscape that is amply supplied with water and compactly covered with vegetation. Adapted from Pokorný [13]



Up to 70–80% of the net radiation can be dissipated by evapotranspiration. The amount of water evaporated from a plant stand can be higher than that evaporated from an open water surface. The amount of water used in evapotranspiration differs widely according to the climatic conditions and the type of plant stand, even when all of the stands that are being compared are well supplied with water. Larcher [11] quotes the maximum daily rates of evapotranspiration as being 3–6 mm in pastures, 8–15 mm in wet meadows, and 6–12 mm in reed beds. Herbst and Kappen [9] found extreme values reaching 20 mm in a reed bed. The respective annual sums of water evaporated are about 300–400 mm in pastures, 1,100 mm in wet meadows and 1,300–1,600 mm in reed beds [11]. The direct use of water from rainfall for evapotranspiration also varies according to the climatic conditions and type of plant stand. Direct evaporation of intercepted rainfall significantly contributes to the total evapotranspiration, e.g., in bogs or wetland forests with a dense leaf canopy. In wetlands, e.g., reed beds, the total evapotranspiration may exceed the total rainfall for the same time period by more than 50%. In most terrestrial ecosystems, on the other hand, the total evapotranspiration is usually smaller than the total rainfall, some of which is lost through the discharging of liquid water.

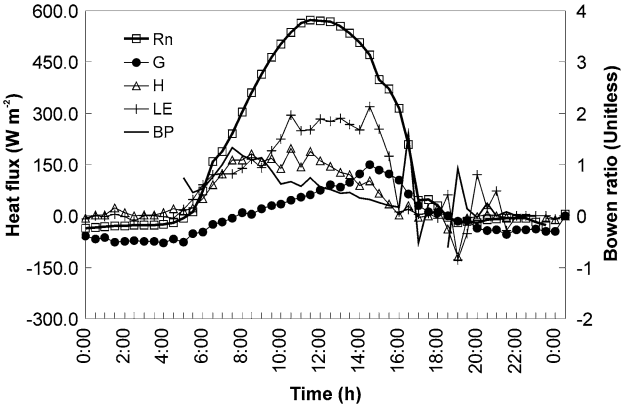


Fig. 5 Daily course of net radiation (*Rn*), ground heat flux (*G*), sensible heat flux (*H*), latent heat flux (*LE*) and Bowen ratio (*BP*), as measured by the eddy covariance method in the Wet Meadows wetland near Třeboň, South Bohemia, Czech Republic, on 18th July 2005

Figure 5 illustrates the transformations and fluxes of solar energy in the wetland ecosystem of the Mokré Louky (Wet Meadows) site near Třeboň (Czech Republic, S. Bohemia) on a bright summer day (18th July 2005). Except for the early morning hours, the transformation of energy into latent heat of evaporation exceeded that into sensible heat, so the resulting Bowen ratio was smaller than 1. A large part of the solar energy input was thus used to cool the ecosystem by evapotranspiration.

The importance of evapotranspiration for cooling the leaves and stand canopies is obvious. By cutting off a leaf, we stop the water supply to it, and the continuing water loss from the leaf results in the closure of stomata and the gradual warming of the leaf. Figure 6 presents photographs of the leaves of *Convolvulus arvensis* L. in the infrared spectral range. As early as 3 min after the leaf is cut off, its temperature starts to exceed that of the intact leaf. Due to

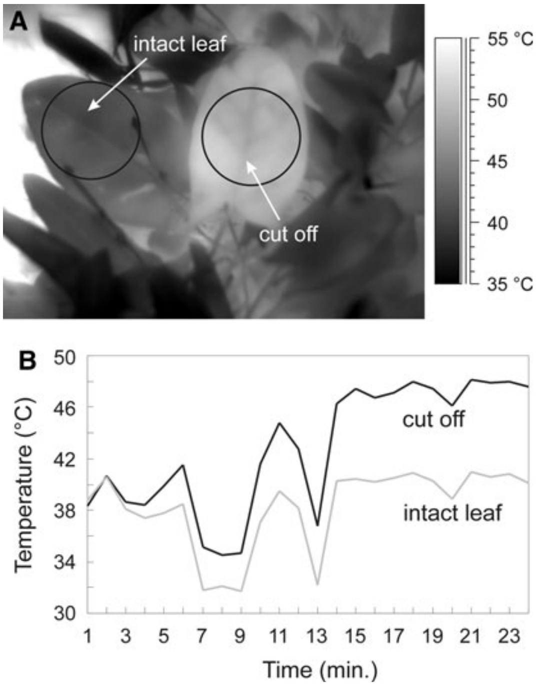


Fig. 6 **a** Infrared images of an intact and a cut-off leaf of *Convolvulus arvensis* L. **b** Evolution of the leaf temperature over time after cutting off the leaf. The fluctuations in temperature are caused by passing clouds

the usually ample water supply available and intensive transpiration, wetland plants act as efficient air-conditioning devices. The leaves of the transpiring plant act as efficient air-conditioning devices with an elaborate system of driving units, the tiny stomata, of which there are usually several tens per 1 mm^2 of leaf area.

The mechanism that cools the climate at a local, regional or even continental scale is the evaporation of water at warm sites and its condensation at colder ones. The shorter the distance between these two types of sites, the shorter the water cycle. A functional landscape with enough water in its wetlands and other ecosystems is therefore well buffered in both space and time with respect to temperature. The intensive recycling of water in a short water cycle also reduces mineral ion losses from the soil [14, 15].

Changes in solar energy and material fluxes caused by drainage

Deforestation and soil drainage result in accelerated water discharge. Simultaneously, the decomposition of soil organic matter (mineralization) is enhanced in a soil in which aeration during dry periods alternates with oxygen deficiency in the wet soil during periods of heavy rainfall. The mineralization of organic matter is linked to the release of H^+ ions (protons), which results in acidification of the soil. Alkaline metal ions such as K^+, Ca^{2+} and Mg^{2+} are thus released into the soil solution. The water-holding capacity of the soil also decreases due to the mineralization of water-binding organic matter (humus). The soil therefore loses water, which flows away as soil solution into running waters and eventually ends up in the sea. From a long-term perspective, these material losses from an ecosystem or landscape are irreversible. The water returns within the large hydrological cycle in the form of clouds originating from water vapor formed above the sea. The material losses from drained agricultural soils reach values as high as several hundreds of kilograms per hectare per year [16]. The water cycle, the dissipation of solar energy, and the retention of substances in the landscape are closely coupled with one another.

At present, climate change is characterized by an increased frequency of cyclones, gales, downpours and long alternating periods of either drought or water surplus. The energy of the gales and other weather extremes originates from spatial temperature and air-pressure differences. We have already shown how vegetation richly supplied with water can effectively damp temperature differences in both space and time at an intensity of several hundreds of watts per square meter [3].

The drainage of large areas causes surprisingly large amounts of sensible heat to be released into the atmosphere. A drop in evapotranspiration by 1 l m^{-2} (equivalent to about 700 Wh) is capable of increasing the daily flux of sensible heat about 40 times more effectively (by 70 W) than the quoted effect of greenhouse gases [radiative forcing, Intergovernmental Panel on Climate Change (IPCC); see the "Appendix"]. For example, a drop in evapotranspiration of 1 mm in the territory of the Czech Republic (79,000 km^2) within a single day releases a comparable amount of sensible heat to the annual production of electric energy in all Czech power plants (about 60,000 GWh).

The main energy fluxes coupled with the solar energy transformations in the vegetation are directly measurable. The real amplitudes of these energy fluxes can be derived from data on the daily or seasonal amounts of evapotranspiration.

Quantitative data on the effects of drainage, deforestation and desertification

In the present world, far-reaching changes in the distribution and dissipation of incoming solar energy are due to large-scale human-induced changes in the water regimes of extensive landscape segments, such as catchment areas. According to the FAO (the United Nations' Food and

Agriculture Organisation), the Earth loses about 200,000 km^2 of agricultural land per year as a result of increasing water shortages. Of this area, 60,000 km^2 are subject to desertification. FAO claims that 30–40% of the land areas of all continents (6.45×10^7 km^2) suffer from water shortages. This means that about one-third of the world's land area is not capable of sufficiently damping the daily pulses of solar energy input and the resulting spatial and temporal differences in heat potential.

In developed countries, the area covered by impermeable substrates is steadily increasing. In Germany, for example, the area of impermeably paved, asphalted or concrete-covered land is increasing by 1 km^2 every day! The "development" of wetlands, especially local and small ones, results in the desiccation of the landscape, and even vegetated areas such as forests are losing their ecosystem functions as well as their utility to mankind because of a lack of water. No record is kept of these ecological and economic losses. Since the 1980s, remote sensing techniques have provided the most efficient tool for detecting and recording such landscape changes, some of which can then be mitigated.

In the developing countries, many of them in Africa, one of the main problems is the loss of a well-functioning vegetation cover resulting from the introduction of European breeds of cattle; large herds of sheep and goats are maintained. The result has been great damage to or even the destruction of vegetation, large-scale erosion, and severely decreased water retention of the landscape. In the heat balances of these areas, the sensible heat flux notably prevails. In Australia, about 1 million hectares are affected in this way. In East Africa, a continuous belt of tropical rainforest has been reduced to a few fragments, each occupying only several hundreds of km^2 at most. In Kenya and Ethiopia, for example, forests now cover only 2% of the total area of these two countries [18]. Wetland areas have also been substantially curtailed there. Again, these landscape changes greatly increase the average Bowen ratio, and have other far-reaching ecological and socio-economic consequences.

Conclusions

Energy and heat fluxes, transformations and exchanges in the biosphere are coupled to vital biological structures and processes. They have a feedback relationship with the solar energy input and are coherently interconnected with one another in a way that enables the effective dissipation of the incoming energy, thus damping temperature extremes. In this respect, vegetation plays a key synergistic role that can be best demonstrated in wetlands. Evapotranspiration, photosynthesis, and heat accumulation in the biomass and soil transform the solar energy and diminish the sensible heat flux and the spatial and temporal temperature differences caused by this component of the heat balance. Vegetation that is capable of repeated renewal thus directly counteracts global warming, reduces the extent of soil erosion, and provides biomass that represents the main food and energy resource for all heterotrophs and is an important link in geobiochemical cycles. Last but not least, its healthy development substantially contributes to the preservation of our planet's biodiversity.

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Appendix

According to materials from the IPCC, the radiative forcing due to the enhanced concentrations of greenhouse gases in the atmosphere has risen by 1–3 W m^{-2} since the start of the Industrial Revolution. According to models of climate change derived by the IPCC, the radiative forcing will increase by 0.2 W m^{-2} in 10 years, i.e., by 1 W m^{-2} in 50 years. These increases are within the range of parts per ten thousand of the solar constant, so they cannot be measured and have only been predicted by a model.

Returning water to the landscape and restoring permanent vegetation results in more effective solar energy dissipation in primary production processes (units of W m^{-2}), reduces air pressure and temperature differences (hundreds of W m^{-2}), slows down the rate of decomposition and thus reduces the heat released by them (units to tens of W m^{-2}), and increases energy uptake and fixation by ecosystems and the use and dissipation of this energy by various ecosystem processes.

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