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*See also:* Biological Nitrogen Fixation; Excretion.

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# Fire

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## Introduction

A global view of potential vegetation distribution based on climate shows large discrepancies with actual vegetation distribution. Fire is often responsible for such discrepancies and on many landscapes it is a major determinant of vegetation distribution. Traditionally fire has been thought of as a disturbance, much like treefalls or floods. However, fire is a predictable ecosystem process that often plays a determining role in community structure and function. Placing fire in its proper role in ecological theory would treat it much like a herbivore in the trophic pyramid, consuming biomass and competing with biotic consumers for resources.

Fossil evidence is clear that as an ecosystem phenomenon, fire dates at least to the Mesozoic over 100 Ma. Indeed, long before our current ecosystems were in place, fire was shaping plant traits and landscapes. For example, tree ring patterns in Jurassic-age fossils suggest a Mediterranean climate of mild winter rain and summer drought, conditions conducive to wildfires and charred fossil fragments illustrate fires were part of these ecosystems. Various fossil evidence has not only shown fires were widespread at this time but different lines of evidence support a similar range of fires as found today, from light surface burning in the understory of forests to high-intensity crown fires in lower-stature woodlands and shrublands.

However, these records do not necessarily demonstrate fire was an important ecosystem process. The first evidence in the geological record of major ecosystem changes driven by fire is from the late Tertiary Period. Massive $C_4$ grassland expansion between 4 and 7 Ma may be the first example of an extensive fire influence in shaping global ecosystems. At this time in subtropical regions there is a clear isotopic signal in soils pointing toward a switch from woodlands to grasslands, coinciding with marked increases in charcoal deposition. Although this coincided with increased climatic seasonality, climate alone cannot explain these changes since in many cases grasslands moved from more arid environments into more mesic ones, something likely only driven by the destructive force of fires.

In order to understand what conditions promote fire as an important ecosystem process, we need to consider the characteristics shared by fire-prone ecosystems today. One way to illustrate this is with a modification of the classical fire triangle (**Figure 1a**) with a triangle better describing the ecological distribution of fire (**Figure 1b**). In order for fire to be a predictable ecosystem feature the following conditions must be met. There must be sufficient moisture and warmth to generate primary productivity capable of providing the fuels necessary to spread fire from one place to another. If productivity is very low, such as in a desert, fires are unlikely due to insufficient biomass. However, high primary productivity alone is insufficient because fire is unlikely unless there is

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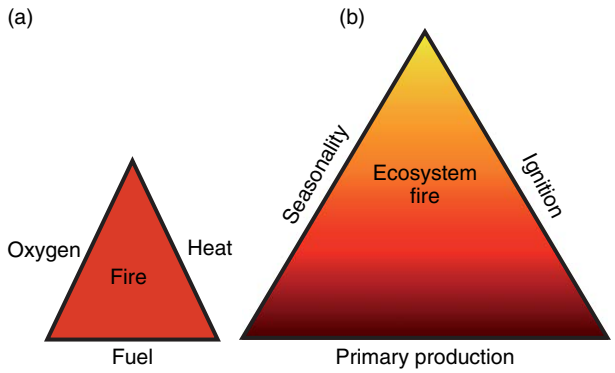


**Figure 1** (a) Traditional fire triangle on the three components necessary for fire and (b) modified to describe the necessary components to describe the ecological distribution of fire.

seasonality sufficient to dry these potential fuels and convert them into fuels available for burning. For example, lowland tropical rainforests outperform most other ecosystems in primary production because they are constantly moist; these potential fuels seldom dry sufficiently to become fuels available for burning. Lastly, given sufficient available fuels at some time of the year, there must be a source of ignition coincident with the availability of fuels. In nature the primary source of ignition is lightning, and regions differ markedly in the importance of lightning (**Figure 2**). However, today, humans have surpassed lightning as the source of fire ignition in many parts of the world.

## Fire Regimes

The 'ecosystem fire triangle' requires coupling primary productivity, seasonality, and ignitions. However, in order to understand fire effects on ecosystems one must view this within the context of gradients in productivity and ignitions, which dictate different fire regimes. Fire regime is best defined in terms of five factors: (1) fuel consumption patterns, (2) intensity and severity, (3) fire frequency, (4) patch size, and (5) seasonality.

### Fuel Consumption Patterns

Fires may consume different fuels due in large part to the vertical and horizontal distribution of plant structures. 'Surface fires' are spread by fuels that are on the ground, which can be either living herbaceous biomass or dead leaf and stem material. Often these occur in forests where the trees hold their canopies aloft and out of reach of the flames. Alternatively, 'crown fires' burn in the canopies of trees or shrubs. Forests are commonly characterized by either a surface fire or crown fire regime, but in other forests mixtures of both fire types occur. Sometimes fires burn through organic matter underground and these are termed 'ground fires', which spread slowly and can last for months, particularly on sites with peat substrate such as swamps during severe droughts.

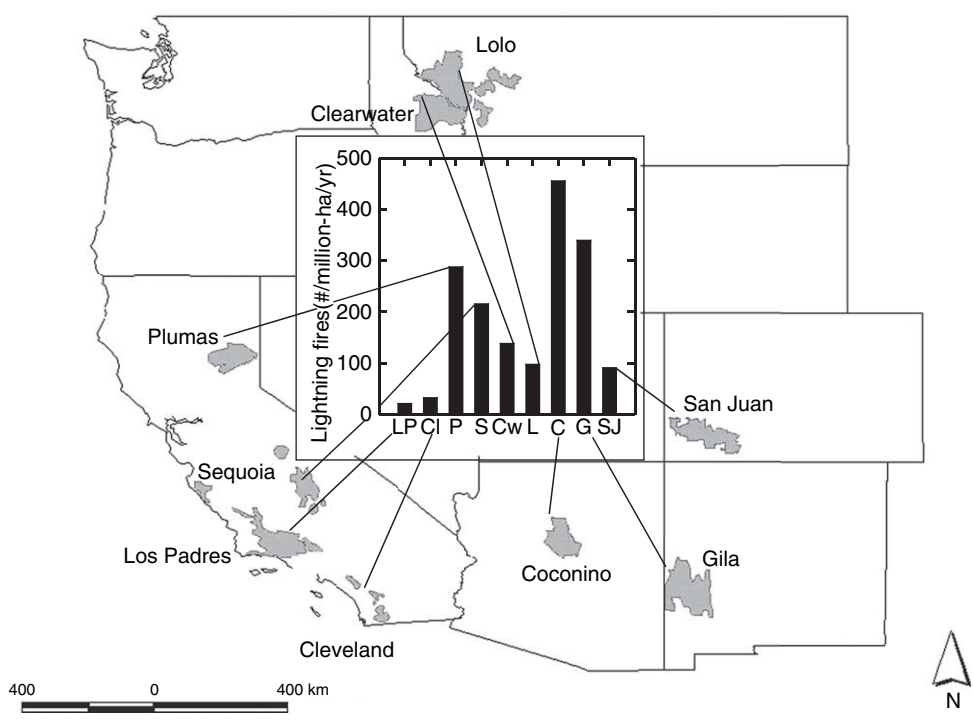


**Figure 2** Distribution of lightning in selected national forests of the western US.

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## Fire Intensity and Severity

Fire intensity describes the energy released from the fire or characteristics of the fire behavior such as flame length and rate of spread. Fire severity refers to the ecosystem impacts of a fire such as mortality of trees or loss in biodiversity.

A widely used measure of fire intensity is fireline intensity, which is the rate of heat transfer per unit length of the fire line (measured in $kW\,m^{-1}$) and represents the radiant energy release in the flaming front. Fireline intensity is a good measure of how likely the fire is to propagate and how difficult it will be to stop, and thus it is a critical component of fire behavior models used to inform fire-suppression activities. Very seldom is fireline intensity actually measured, rather it is generally inferred based on flame length, which has been found to correlate with fireline intensity; however, this correlation has not been widely tested.

Fire severity measurements vary depending on the ecosystem. In forests, fire severity is measured in terms of tree mortality, canopy loss, or bole and crown scorch. These measures of fire severity are often interpreted as surrogate measures of fire intensity. It is assumed that these reflect the impact of the fire on ecosystem properties such as its ability to recover. Fire severity measures used in forests are not generally relevant to shrublands, where all aboveground biomass is killed in crown fires. In such crown fires ecosystem indicators of fire severity that may be useful measures of ecosystem impact are resprouting success and seed bank survivorship. However, the linkage between fire intensity, fire severity measures, and ecosystem impact are complex and largely unexplored. A number of studies have found that in California chaparral shrublands indicators of fire intensity are related to diminished cover in the first post-fire growing season; however, these effects were are short-lived. Also, while high fire severity may inhibit regeneration of some species, it is actually correlated with improved regeneration in other species. Fire severity is often a measure used in making assessments of watershed stability after fire, but the relationship between these parameters is not well established for many ecosystems.

## Fire Frequency

Fire frequency is often expressed as the fire rotation interval, which is the time required to burn the equivalent of a specified area. However, on many landscapes some areas receive more fires than other areas and thus a more precise measure is the fire return interval, which is the spatially specific time between fires in a specified area. For example, coastal mountains in southern California have a fire rotation interval of about 35 years but some specific sites have a fire return interval of one fire every 5 years and others every 50 years.

Our understanding of historical fire frequency is better for some ecosystems than for others. In surface fire regimes such as ponderosa pine forests of the Southwestern US, low-intensity fires burn and sometimes scar trees (**Figure 3**) but do not typically kill the trees. Thus, scarred trees can be used as a record of past fires by relating past scars to particular growth rings in the tree. Such trees commonly provide fire records back to 200–300 years. In the giant sequoia forests of Sequoia National Park in California, studies have documented fire frequencies back to more than 2000 years.

Much longer records of past fires have been obtained by examining soil cores from lakes and bogs. Under certain conditions one can obtain an approximate date for a particular layer of a soil core and measure the amount of charcoal, thus providing a relative measure of fire activity over time. While this technique is capable of providing records back to over 10 000 years ago, the resolution and certainty of burning are less than that with tree ring studies. Fire frequency estimates based on charcoal deposition are affected by the pattern of dispersion of charred particles, and fuel type, as well as rainfall that affects sediment movement. Thus, these records can be interpreted

**Figure 3** Fire scar at the base of a western US conifer.

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differently by different investigators. Even less direct measures of fires include geological studies of past debris flows that likely resulted from very large and severe wildfires.

For many ecosystems the only reliable source of data on fire history comes from written records maintained by fire management agencies. In the US these often go back to the early decades of the twentieth century. Over time the quality of these records has likely improved by better observations and improved techniques and thus these historical records must be interpreted cautiously.

### Fire Patch Size

Fire size varies tremendously, from a lightning-ignited fire that remains localized around a particular tree it strikes to massive forest fires that cover many square miles. In general the vast majority of landscape that burns is the result of just a small percent of the total number of fires. Many forest fires have complicated patterns of fuel consumption resulting from a mixture of surface fires, crown fires, and unburned patches. This heterogeneity is important to ecosystem processes such as tree recruitment for reasons to be discussed below. Heterogeneity is also important for wildlife since many species utilize plant resources available in recently burned areas but require unburned forest or shrubland patches for cover and breeding sites.

### Fire Seasonality

The occurrence of season fires varies as a function of climatic differences. For example, Florida wildfires are common during the winter because it is relatively dry at that time, whereas summers are moist and often unsuitable for burning. Monsoon environments such as in the Southwestern US have fires concentrated in late spring and early summer because fuels are dry and the arriving monsoon storms provide a ready source of ignitions. In contrast the bulk of burning in Mediterranean-climate California tends to be in the late summer and early fall after a very extended drought of 6 months or more. Today humans have the potential of igniting fires out of the natural fire season and can alter ecosystems by increasing the length of the fire season and frequency of burning. Sometimes natural recovery processes are compromised by out-of-season burning.

## Fire Impacts and Recovery

Surface fires and crown fires not only have different impacts on ecosystem processes but also have different impacts on the evolution of plant traits.

### Surface Fire Regimes

Ponderosa pine forests of the Southwestern US typify this regime. Productivity is sufficient to allow trees to grow fast enough to, in effect, escape the flames of surface fires. This strategy requires that trees also evolve thick bark to withstand high temperatures around those parts of the plant directly exposed to flames. In addition, trees must drop dead branches (termed self-pruning) otherwise these would carry fire from the surface into the canopy. Under natural conditions, as trees grow in size they become increasingly resistant to being completely killed by fire. However, because surface fuels heat the soil surface intensely, seeds dispersed prior to the fire are typically killed, thus regeneration from seeds in the soil prior to the fire is relatively limited.

For many of the dominant trees reproduction is poor in unburned forests because of the thick surface litter that inhibits seedlings from reaching the soil surface and because the shade of the tree canopy inhibits seedling growth. Trees like ponderosa pine require open gaps, such as produced by fire, but the parent trees must survive fire in order to provide seeds after the fire that created the gap has passed. Even in surface fire regimes small gaps are created by localized crown fires that may comprise a few to many trees being torched, and these are important sites for tree regeneration. These high light gaps are ideal establishment sites for pine seedlings and the extent to which establishment occurs is a function of the proximity of parent trees.

Gap size is very critical to successful regeneration. If gaps are very small they have a higher probability of accumulating sufficient fuels to carry a repeat fire before the saplings have developed sufficiently to withstand a repeat fire. However, if gaps are very large the probability of seeds reaching the site from trees that survived the fire is diminished, and for areas with large crown fires of thousands of hectares, natural regeneration of the original forest cover may require centuries. Of course, while foresters may consider such events as undesirable, they are a natural part of most ecosystems and there is a diversity of shrub and herb species that depend on such conditions for their long-term persistence.

### Crown Fire Regimes

California chaparral shrublands and Northern Rocky Mountain lodgepole pine forests typically burn as crown fires, where fire spread is through the canopy of the dominant life forms. In these ecosystems fires burn much of the aboveground biomass leaving what often appears as denuded landscapes. Recovery of these ecosystems is largely endogenous, meaning the regeneration stock is still present on the completely burned landscape and there is limited dependence on survival of outside

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stock, as in the case of ponderosa pine forests. In chaparral the vast majority of species regenerate rapidly by resprouting new shoots from the base of burned stems. In addition, many of the dominate species possess dormant seed banks that have accumulated for decades in the soil. These seeds are triggered in unison to germinate after fire by cues such as intense heat or smoke. Both of these regeneration modes are favored by the fact that there are relatively limited fuels on the soil surface and most of the intensity of the fire is held aloft in the canopies of the shrubs, thus, limiting the mortality of seeds and rootstocks.

One important ecosystem property of this fire regime is that regeneration is independent of the pattern of burning. Recovery after fire is not affected by the size of the fire and these ecosystems recover well after massive landscape burns that consume thousands of hectares of shrubland. Indeed, in some cases small localized burns are detrimental to recovery because the unburned landscape harbors many herbivores that can decimate post-fire regeneration.

In northern latitudes forest growth is often stunted due to a very short growing season and these forests have many similarities to chaparral shrublands. Examples include Rocky Mountain lodgepole pine and forest jack pine forests. Under these conditions of lower growth rates, coupled with typically very high lightning fire density, the trees seldom can outgrow the surface fuels and thus succumb to crown fires. Some of the dominant trees have developed dormant seed banks much like in chaparral, but rather than being stored in the soil they are held in the canopy in serotinous cones that remain closed until heated by fire.

## Fire, Weather, and Climate Interactions

Weather and climate affect fires in quite different ways, the former affects fire behavior and the latter affects the fuels consumed by the fire.

### Fire Weather

Weather refers to the conditions at the time of a fire and largely affects the behavior of the fire. The primary weather variable that most affects fires is wind. At low wind speed, fuel structure plays a critical role in fire spread. Live foliage dissipates heat by losing water and often will not combust until it has been heated sufficiently to drive off water. In the absence of wind this typically requires the presence of dead fuels, which combust more readily and will heat living fuels sufficiently to combust. Fire spread commonly depends upon a sufficient mixture of live and dead fuels in order to sustain the fire. However, under windy conditions this equation changes and wind is capable of carrying heat to living foliage and rapidly spreading fire through mostly living foliage. Wind increases combustion by mixing of oxygen and altering the flame angle so that there is increased heating of fuels ahead of the flaming front. In general, as wind speed increases the role of fuels diminishes. Weather patterns that lead to high winds are a major determinant of fire size and essentially all large fires on contemporary landscapes are the result of severe fire weather conditions coupled with high temperature and low humidity.

On some landscapes weather may be of such overriding importance that it obscures climate signals that influence fire regimes in many parts of North America. For example, predictable annual autumn foehn winds in southern California are the primary determinant of large fires, and consequently droughts show little or no relationship to annual variation in area burned. However, outside the autumn foehn wind season droughts are associated with a lengthening of the fire season.

### Fire Climate

Climate, which in this context refers to the antecedent conditions prior to fire, works largely through changing fuels. The most immediate effect of climate is when drought conditions cause the drying of fuels to the point where living foliage combusts almost as readily as dead foliage. Under drought conditions there is commonly an increased incidence of fire in the subsequent fire season (**Figure 4**). Climate, however, can have longer-term impacts by affecting primary production and the quantity of fuels. This is most evident in forests where herbaceous plants are the primary fuels responsible for fire spread. When very high rainfall years produce luxuriant herb growth, this flush of herbs will eventually die and increase the probability of burning 1 or 2 years later (**Figure 4b**). Forests with surface fire regimes driven by dead leaves and branches on the forest floor do not exhibit this delayed response to anomalously high rainfall years (**Figure 4a**).

Historical climate signals are responsible for regional synchrony in fire activity evident in increased fire frequency and fire size during the Medieval Warm Period (1000–650 yr BP) in the western US. The cooler and drier conditions of the Little Ice Age (500–100 yr BP) may be responsible for greater fire frequency compared to the less-frequent fires of the warmer moister conditions of the twentieth century.

A number of ocean–atmosphere patterns (e.g., El Nino southern oscillation (ENSO) or the southern oscillation) that have been discovered in recent decades by climatologists have been implicated in long-term patterns of fire behavior. These patterns are often evident over decades, and suggest some level of periodicity in fire behavior that may be useful in interpreting the past and planning for the future.

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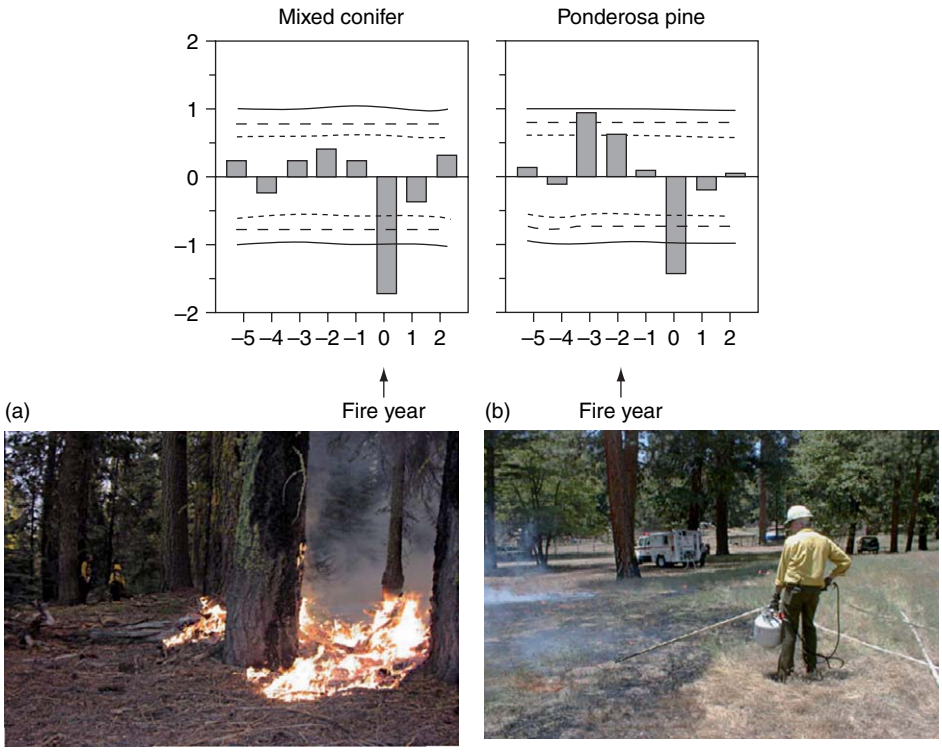


**Figure 4** Relationship of fire to climate in two forest types with surface fire regimes driven by (a) dead litter and (b) herbaceous fuels. Climate diagrams plot the Palmer Drought Index on the *y*-axis (positive numbers indicate moist years and negative numbers drought years). Bars represent the degree of drought and the *x*-axis the fire year (0) or years prior to or after fire. Horizontal dotted, dashed, and solid lines are 99.9, 99.0, and 95.0 confidence intervals, respectively. From Swetnam TW and Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate* 11: 3128–3147.

## Human Disruptions of Natural Fire Regimes

Humans have had a multitude of impacts on natural fire regimes. Humans put out fires and humans start fires and the net effect varies with the ecosystem.

### Fire Suppression

In the US, fire suppression policy directed at putting out all fires as rapidly as possible has been practiced for much of the twentieth century. The effectiveness of fire suppression has varied temporally and spatially with relatively ineffective suppression early in the twentieth century but increasingly more effective later on. Fire suppression was immediately effective in areas of ready access, where fires could be discovered early and resources deployed quickly to extinguish them. In more remote areas, suppression policies did not have much impact on fire behavior until development of the fire lookout system in the 1930s facilitated early fire detection and the smoke jumping program in the 1940s facilitated access. Thus, in many remote locations fire suppression policies have significantly altered fire regimes only in the latter half of the twentieth century.

The extent to which fire suppression policy has affected ecosystems is linked to fire regime. Many coniferous forests historically exposed to frequent fires have had fire excluded for a century or more. This is well demonstrated by fire histories from fire-scarred trees (**Figure 3**) in southwestern ponderosa pine, where fire-scar records indicate frequent fires until the late nineteenth century, and then a cessation of burning throughout the twentieth century. Much of this is due to the unique conditions of these fire regimes. Fires typically burn surface fuels with short flame lengths that pose little threat to fire fighters. Also, throughout much of the Southwest fires are still largely ignited by lightning and under weather conditions particularly conducive to rapid suppression.

The effect of fire suppression has changed over time. Throughout the twentieth century the impact was to exclude fire. However, as more and more natural fire cycles were missed, forests have increased in tree density, and many of the saplings have remained suppressed in the understory. This has the unwanted effect of producing ladder fuels capable of carrying surface fires into the canopies of the dominant trees and converting surface fire regimes into crown fire regimes.

In contrast, southern California chaparral landscapes have not had fire excluded over most of the twentieth

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century. Despite the fact that these landscapes were managed by the same fire-suppression policy, and heroic efforts have been directed at trying to suppress fires, the ferocity of these crown fires, particularly when driven by the autumn foehn winds, has made total fire exclusion impossible. This, however, is not to say fire-suppression policy has had no impact on these landscapes. Quite the contrary, this landscape has had more than a century of an anthropogenic fire regime driven by human ignited fires. Without fire-suppression activities these landscapes likely would have had fire frequencies grossly in excess of natural and sustainable levels. On an average fire suppression has managed to maintain this landscape within the historical range of fire frequency, although many localized areas have been hammered with fire to such an extent that they have lost most of all of their native biota and been replaced by non-native grasses and forbs.

### Other Land-Use Impacts on Fire Regimes

Intensive livestock grazing throughout the US has contributed to altered fire regimes since at least the late nineteenth century. The primary effect of grazing is to reduce herbaceous fuels and in many forest types where fires are dependent on surface fuels, grazers outcompete fire for these herbaceous resources. Thus, livestock grazing has the capacity to exclude fire in much the same way as a fire-suppression policy can. In addition to diminishing fuels, livestock grazing reduces grass competition for woody species and thus enhances the recruitment of pines and other trees that contribute to dense thickets of saplings, which act as ladder fuels. Throughout western North America, grazing has been present much longer than fire suppression, and because 70% of the western USA wildlands are currently grazed, it should be considered a widespread factor affecting fire regimes.

Past logging practices have also altered fire regimes, not by excluding fire but by directly altering fuel structure. When the dominant trees in a forest are extracted for commodities, they open the way for extensive recruitment of smaller trees. Under natural conditions this dense thicket of trees would be thinned by fires; however, under modern fire suppression, these thickets remain and pose hazardous fuel conditions. Other effects of logging are to increase surface fuels from the 'slash' of dead branches and needles that may be left on site.

In some forests there is good evidence that fire severity depends more on past logging operations than fire suppression. In some cases this was due to residual flammable slash – for example, the most devastating fire of all times in North America was largely due to poor logging practices. Massive logging slash is considered to have been the major factor in the 1871 Peshtigo Fire that burned 500 000 ha and killed over 1200 people in Wisconsin forests. Thus, it should be recognized that contemporary efforts at reducing fire hazard by increasing logging is only likely to be successful if done in an appropriate manner where slash is removed or burned. Logging complicates our ability to make inferences about the impact of fire suppression on fire behavior since most of the western US ponderosa pine forests were logged at least once.

The fire description given above is generally valid for all fires including the frequent fires in Spain, Portugal, Greece, Australia, and South Africa.

*See also:* Chaparral.

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# Fish Growth

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Processes of Fish Growth
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## Introduction

The more than 3 m long ocean sunfish *Mola mola* develops from an egg that is about a millimeter in diameter. The anadromous brown trout *Salmo trutta* often hatches in a small stream in the midst of a forest, migrates after one or more years into the sea for foraging, and eventually returns as an adult to the natal stream for spawning. As fish grow through their life, they often occupy different habitats, are threatened by different predators, and rely on different food resources. Understanding how these complexities shape lifetime patterns of animal growth is a large and active field of research. In this article, we examine one component of this research by reviewing the most common mathematical models that have been used to describe and interpret the growth of fish. These models have been developed for several purposes, including identifying and comprehending the causes of individual variability, to predict consequences for fisheries yield, and to improve production in fish farming.

Experimental studies and descriptive field-based research have provided valuable insight that has increased our knowledge of fish growth in both the laboratory and the wild. Modeling fish growth is a worthy endeavor because it allows us to better understand the mechanisms underlying how and why a fish grows; it provides a means of calculating parameters that can be readily compared across populations, and we can use these growth models as parts of larger, more comprehensive models to study trophic interactions or ecosystem dynamics. However, modeling has the most to offer when used in conjunction with experiments and field work. In a cyclic manner, models can generate hypotheses for experiments, and experiments can test model assumptions and predictions.

This article only considers models for individual fish growth. Models are also used for describing the growth of an entire fish stock in biomass or abundance, for example, logistic models with exponential population growth limited by a carrying capacity such as in Lotka–Volterra models (see Fishery Models and Growth Models). Such population models underlie general concepts in fisheries science (e.g., the maximum sustainable yield) and are still used in the assessment and management of fish stocks. They do not, however, contain information about individual size, which is a drawback since survival probability and reproductive rates often change as an individual grows. As a consequence, the distribution of individual body sizes in the population will influence population dynamics and the population's overall growth rate. These effects become particularly strong in long-lived species. More recent approaches therefore combine individual growth models of the type described in this article with size-specific rates for survival and reproduction to