Any condition that approaches or exceeds the limits of tolerance is said to be a limiting condition or a limiting factor. Under steady-state conditions, the essential material available in amounts most closely approaching the minimum need tends to be the limiting one a concept that has come to be known as Liebig's "Law" of the minimum.

The idea that an organism is no stronger than the weakest link in its ecological chain of requirements was first clearly expressed by Justus Liebig in 1840. Liebig was a pioneer in studying the effect of various factors on the growth of plants. He found, as do agriculturists today, that the yield of crops was often limited not by nutrients needed in large quantities, such as carbon dioxide and water, since these were often abundant in the environment, but by some raw material, such as zinc, for example, needed in minute quantities but very scarce in soil. His statement that "growth of a plant is dependent on the amount of foodstuff which is presented to it in minimum quantity".

Extensive work since the time of Liebig has shown that two subsidiary principles must be added to the concept if it to be useful in practice.

1. The first is a constraint that Liebig's law is strictly, only under steady-state conditions that is, when inflows balance outflows of energy and materials. To illustrate, suppose that CO_2 was the major limiting factor in a lake, and productivity was therefore in equilibrium with the rate of supply of CO_2 coming from the decay of organic matter. Assume that light, nitrogen, phosphorus and other vital elements were available in excess of use in this steady-state equilibrium. If a storm brought more CO_2 into the lake, the rate of production would change and depend upon other factors as well. While the rate is changing, there is no steady state and no minimum constituent. Instead, the reaction depends on the concentration of all constituents present, which in this transitional period differs from the rate at which the least plentiful is being added. The rate of production would change rapidly as various constituents were used up, until some constituent, perhaps CO_2 again, became limiting. The lake system would once again be operating at the rate controlled by the law of the minimum.
2. The second important consideration is factor interaction. Thus, high concentration or availability of some substance, or the action of some factor other than the minimum one, may modify the rate of utilization of the latter. Sometimes organisms can

substitute, at least in part, a chemically closely related substance for one that is deficient in the environment. Thus, where strontium is abundant, mollusks can substitute strontium for calcium to a partial extent in their shells. Some plants have been shown to require less zinc when growing in the shade than when growing in full sunlight; therefore, a low concentration of zinc in the soil would less likely be limiting to plants in the shade than under the same conditions in sunlight.

Shelford law of tolerance

Limits of tolerance concept: Not only may too little of something be a limiting factor, as proposed by Liebig, but also too much, as in the case of such factors as heat, light and water. Thus, organisms have an ecological minimum and maximum; a range in between represents the limits of tolerance. The concept of the limiting effect of maximum as well as minimum was incorporated into the "law" of tolerance by V.E. Shelford in 1913. Since about 1910, much work has been done in "tolerance ecology", so that the limits within which various plants and animals can exist are known. Especially useful are what can be termed "stress tests" carried out in the laboratory or field, in which organisms are subjected to an experimental range of conditions. Such a physiological approach has helped ecologists to understand the distribution of organisms in nature; however, it is only part of the story. All physical requirements may be well within the limits of tolerance for an organism, and the organism may still fail because of biological interrelations.

Some subsidiary principles to the law of tolerance may be stated as follows:

1. Organisms may have a wide range of tolerance for one factor and a narrow range for another.
2. Organisms with wide range of tolerance for all factors are likely to be most widely distributed.
3. When conditions are not optimum for a species with respect to one ecological factor, the limits of tolerance may be reduced for other ecological factor; the limits of tolerance may be reduced for other ecological factors.
4. Frequently, it is discovered that organisms in nature are not actually living at the optimum range of particular physical factor. In such cases, some other factor or factors are found to have greater importance. For example, certain tropical orchids

actually grow better in full sunlight than in the shade, provided they kept cool. In nature, they grow only in the shade because they cannot tolerate the heat of direct sunlight.

5. Reproduction is usually a critical period when environmental factors are most likely to be limiting. The limits of tolerance for reproductive individual, seeds, eggs, embryos, seedlings and larvae are usually narrower than for non reproducing adult plants or animals. Adult blue crabs and many other marine animals can tolerate brackish water or freshwater that has a high chloride content and thus are often found for some distance up rivers. The larvae, however, cannot live in such waters; therefore, the species cannot reproduce in the river environment and never become established permanently. The geographical range of game birds is often determined by the impact of climate on eggs or young rather than on the adults. One can cite hundreds of other examples.

For the relative degree of tolerance, a series of terms have come into general use in ecology that use the prefixes steno- meaning “narrow” and eury- meaning “wide”. Thus,

Stenothermal-eurythermal	refers to temperature
Stenohydric-euryhydric	refers to water
Stenohaline-euryhaline	refers to salinity
Stenophagic-euryphagic	refers to food
Stenoecious-euryecious	refers to habitat selection

As an example, let us compare the conditions under which brook trout (*Salvelinus*) eggs and leopard frog (*Rana pipiens*) eggs will develop and hatch. Trout eggs develop between 0^0 and 12^0C with optimum at about 4^0C. Frog eggs will develop between 0^0 and 30^0C with optimum at about 22^0C. Thus, trout eggs are stenothermal, low temperature tolerant compared with frog eggs, which are eurythermal, both low and high temperature tolerant. Trout in general, both eggs and adults, are relatively stenothermal, but some species are more eurythermal than is the brook trout. Likewise, of course, species of frogs differ. These concepts, and the use of terms in regard to temperature, are illustrated in figure. Steno organisms often become very abundant when their conditions are favorable and stable

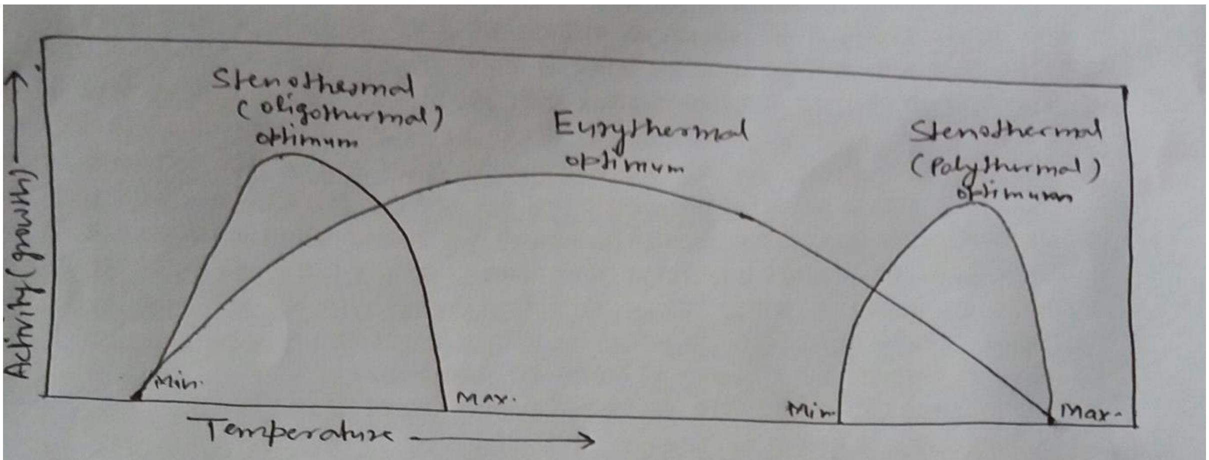

Fig: Comparison of the relative limits of tolerance of stenothermal and eurythermal organisms. Minimum, optimum and maximum lie close together for a stenothermal species, so that a small difference in temperature, which might have little effect on a eurythermal species, is often critical. Note that stenothermal organism may be either low-temperature tolerant (oligothermal) or high-temperature tolerant (polythermal).

<u>Combined concept of limiting factors</u>

The presence and success of an organism or a group of organism depends upon a complex of conditions. Any condition which approaches or exceeds the limits of tolerance is said to be a limiting condition or a limiting factor.

By combining the idea of the minimum and the concept of limits of tolerance we arrive at a more general and useful concept of limiting factors. Thus, organisms are controlled in nature by

(1) The quantity and variability of materials for which there is a minimum requirement and physical factors which are critical, and
(2) The limits of tolerance of the organisms themselves to these and other components of the environment.

The chief value of the concept of limiting factors lies in the fact that it gives the ecologist an “entering wedge” into the study of complex situations.

Environmental relations of organisms are apt to be complex, so that it is fortunate that not all possible factors are of equal importance in a given situation or for a given organism. Some strands of the rope guiding the organism are weaker than others. In a study of a particular situation the ecologists can usually discover the probable weak links and focus his attention, initially at least, on those environmental conditions most likely to be critical or limiting. If an organism has a wide limit of tolerance for a factor which is relatively constant and in moderate quantity in the environment, that factor is not likely to be limiting. Conversely, if an organism is known to have definite limits tolerance for a factor which also is variable in the environment, then that factor merits careful study, since it might be limiting.

For example, oxygen is so abundant, constant and readily available in the terrestrial environment that it is rarely limiting to land organisms. On the other hand, oxygen is relatively scarce and often extremely variable in water and is thus often an important limiting factor to aquatic organisms, especially animals. Oxygen, of course, is just as vital a physiological requirement for most land organisms as for most water organisms, but from the ecological point of view it is rarely limiting on land.

Reference:

1. Eugene P. odum: Basic Ecology