

Influences of Riparian Vegetation on Aquatic Ecosystems with Particular Reference to Salmonid Fishes and Their Food Supply^{1,2}

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Abstract.--The riparian zone has important influences on the total stream ecosystem including the habitat of salmonids. Shade and organic detritus from the riparian zone control the food base of the stream and large woody debris influences channel morphology. Temporal and spatial changes in the riparian zone, the indirect influences of riparian vegetation on salmonids, and the effects of man's activities are discussed.

INTRODUCTION

Streamside vegetation strongly influences the quality of habitat for anadromous and resident coldwater fishes. Riparian vegetation provides shade, preventing adverse water temperature fluctuations. The roots of trees, shrubs, and herbaceous vegetation stabilize streambanks providing cover in the form of overhanging banks. Streamside vegetation acts as a "filter" to prevent sediment and debris from man's activities from entering the stream. Riparian vegetation also directly controls the food chain of the stream ecosystem by shading the stream and providing organic detritus and insects for the stream organisms.

¹Contributed paper, Symposium on the Importance, Preservation and Management of the Riparian Habitat, July 9, 1977, Tucson, Arizona.

²The work reported in this paper was supported in part by National Science Foundation Grant No. 7602656 to the Coniferous Forest Biome and Grant No. BMS75-07333 to the River Continuum Project. This is contribution No. 283 from the Coniferous Forest Biome and No. 5 from the River Continuum Project.

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WHAT IS RIPARIAN VEGETATION?

Riparian vegetation is at the interface between aquatic and terrestrial environments. It has, therefore, been defined and examined from a number of perspectives. Plant ecologists speak in terms of riparian species and plant communities. The riparian zone may also be defined geographically in terms of topography, soils, and hydrology. We prefer to take a functional approach; that is, to consider riparian vegetation as any extra-aquatic vegetation that directly influences the stream environment.

Consequently, in defining riparian vegetation we must consider the full scope of its biological and physical influences on the stream. Riparian vegetation regulates the energy base of the aquatic ecosystem by shading and supplying plant and animal detritus to the stream. Shading affects both stream temperature and light available to drive primary production; therefore, the balance between autotrophy and heterotrophy is determined by multiple functions of riparian vegetation.

Although imperfect, the stream order system (Leopold et al. 1964) is a useful way to classify elements of a drainage system. In small and intermediate-sized streams (up to about fourth-order) in the Pacific Northwest, riparian vegetation exercises important controls over physical conditions in the stream environment. Rooting by herbaceous and woody vegetation tends to stabilize streambanks, retards erosion, and, in places, creates over-

hanging banks which serve as cover for fish. Above ground woody riparian vegetation is an obstruction to highwater streamflow, sediment and detritus movement, and is a source of large organic debris. Large organic debris in streams (1) controls the routing of sediment and water through the system, (2) defines habitat opportunities by shaping pools, riffles, and depositional sites and by offering cover, and (3) serves as a substrate for biological activity by microbial and invertebrate organisms (Triska and Sedell 1976; Swanson et al. 1976; Sedell and Triska 1977; Anderson et al. in press).

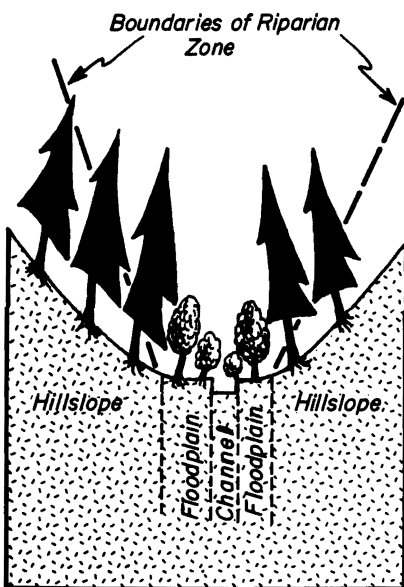
The influences of riparian vegetation on coniferous forest stream ecosystems in the Pacific Northwest are summarized in figure 1. In a functional approach to defining riparian vegetation, all floodplain vegetation as well as trees on hillslope areas which shade the stream or directly contribute coarse or fine detritus to it are considered part of the riparian zone. In the Pacific Northwest, vegetation in the zone of riparian influence includes herbaceous ground cover, understory shrubby vegetation (commonly deciduous), and overstory trees on the flood plain (generally deciduous) and on hillslopes (generally coniferous).

VARIATIONS OF THE RIPARIAN ZONE IN TIME AND SPACE

The character and importance of riparian vegetation varies in time and space. Temporal variation involves patterns of vegetative succession following disturbances. Major processes of vegetation disturbance include wildfire and clearcutting (important to upslope vegetation) and damage due to impact of sediment and floating ice or organic debris during flood flows. Spatial variation occurs along the continuum of increasing stream size from small headwater streams to large rivers.

Temporal Variations of Riparian Zones

The effectiveness of a riparian zone in regulating input of light, dissolved nutrients, and litterfall to the stream varies through time following wildfire, clearcutting, or other disturbances (fig. 2). In the first decade or two following deforestation, streamside vegetation may increase in height growth and biomass more rapidly than upslope communities. Shading of the stream by riparian vegetation gradually diminishes the potential for aquatic primary production until maximum canopy closure. Deciduous shrubs and trees within the riparian zone will contribute most



RIPARIAN VEGETATION		
SITE	COMPONENT	FUNCTION
above ground-above channel	canopy & stems	<ol style="list-style-type: none"> 1. Shade-controls temperature & in stream primary production 2. Source of large and fine plant detritus 3. Source of terrestrial insects
in channel	large debris derived from riparian veg.	<ol style="list-style-type: none"> 1. Control routing of water and sediment 2. Shape habitat-pools, riffles, cover 3. Substrate for biological activity
streambanks	roots	<ol style="list-style-type: none"> 1. Increase bank stability 2. Create overhanging banks-cover
floodplain	stems & low lying canopy	<ol style="list-style-type: none"> 1. Retard movement of sediment, water and floated organic debris in flood flows

Figure 1.--Extent of riparian zone and functions of riparian vegetation as they relate to aquatic ecosystems.

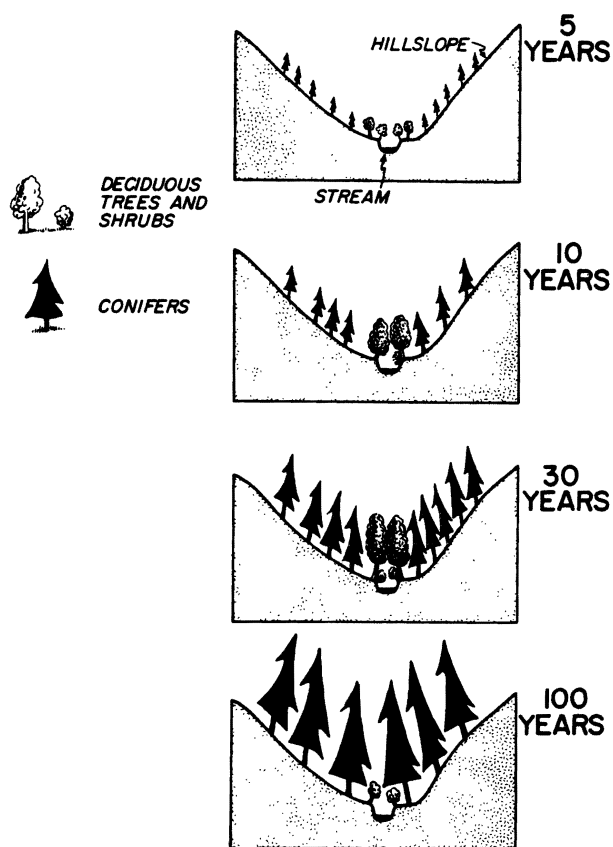


Figure 2.--Changes in the riparian zone through time.

of the litter inputs during early watershed recovery. These deciduous inputs will more readily decompose than coniferous litter which dominates inputs late in watershed recovery and in old-growth forests (Sedell et al. 1975; Triska and Sedell 1976).

The temporal development of riparian zones causes a shift in the energy base of the stream from algae to deciduous leaves to a combination of deciduous and coniferous leaves. The last stage in riparian succession is a complex mosaic of coniferous overstory, deciduous shrub layer, and herbaceous ground cover. Streams flowing through older, stratified forests receive the greatest variation in quality of food for detritus-processing organisms. Herbaceous vegetation is high in nutrient content, low in fiber, and utilizable by stream organisms as soon as it enters the stream. Leaves from the deciduous shrub layer are higher in fiber content and take 60 to 90 days after entering the stream to be utilized fully by stream microbes and insects. The conifer leaves take 180-200 days to be processed. Thus there is a sequencing of utilization of inputs from these

three distinctive riparian strata. The results for the stream are rich and diverse populations of aquatic insects which are keyed into the timing and varied quality of the detrital food base.

Spatial Variation of Riparian Zones

A stream should be viewed as a continuum from headwaters to mouth (Vannote, personal communication; Cummins 1975, 1977). The influence and role of riparian vegetation will vary with stream order and position along the continuum. Some broad characteristics of streams and rivers are depicted diagrammatically in figure 3.

Extensive networks of small first to third order streams comprise about 85 percent of the total length of running waters (Leopold et al. 1964). These headwater streams are maximally influenced by riparian vegetation (the ratio of shoreline to stream bottom is highest), both through shading and as the source of organic matter inputs. Even in grasslands, the distribution of trees and shrubs follows perennial and, occasionally, intermittent watercourses except where land use practices have resulted in removal or suppression of riparian vegetation.

These low light, high gradient, constant temperature headwater streams receive significant amounts of coarse particulate matter (CPOM > 1-mm diameter). Their most striking biological features are the paucity of green plant life or primary producers (algae and vascular plants) and the abundance of invertebrates that feed on CPOM (Cummins 1974, 1975). Shredders reduce detritus particle size by feeding on CPOM and producing feces which enter the fine particulate organic matter (FPOM < 1-mm diameter) pool.

Although the transition is gradual and varies with geographical region, the shift from heterotrophy to autotrophy usually occurs in the range of third- to fourth-order streams (fig. 3). Rivers in the range of fourth- to sixth-order are generally wide and the canopy of riparian vegetation does not close over them. Direct inputs of CPOM from the riparian zone are lower in larger rivers because of the reduced ratio of length of bank to area of river bottom.

The importance of floodplain vegetation (mainly deciduous) increases relative to the hillslope species (mainly coniferous) and in a downstream direction. Generally this is so because the floodplain width increases downstream and the canopy opening over larger streams allows greater arboreal expression of deciduous riparian vegetation. Development of deciduous riparian trees is suppressed by shade along small streams.

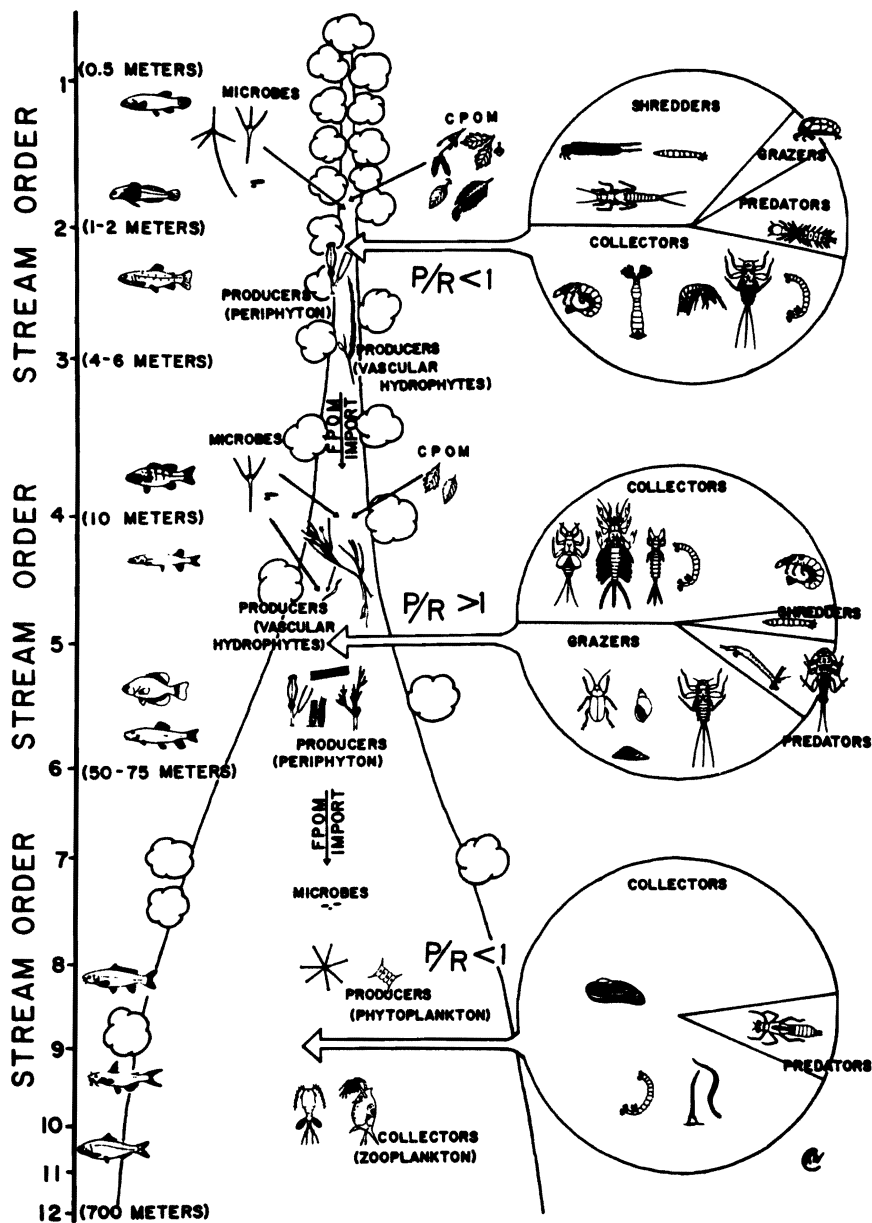


Figure 3.--A diagrammatic representation of some of the changes that occur in running water systems from headwaters to mouth. The organisms pictured are possible representatives of the various functional groups occurring in the size ranges of streams and rivers. Although a large network of smaller tributaries coalesce into larger rivers, the system is shown diagrammatically as a single headwater through all orders to the river mouth (orders and approximate ranges of stream or river width are shown at the left margin). The decreasing direct influence of the adjacent terrestrial vegetation of the watershed and increasing importance of

inputs from upstream tributary systems is a basic feature of the conceptual scheme. The proportional diagrams at the right show the changes in relative dominance of invertebrate functional groups from headwaters to mouth. Important shredders include certain species of stoneflies, caddisflies, and craneflies that feed on CPOM (coarse particulate organic matter). Dominant collectors are net-spinning caddisflies, blackflies, clams, and certain midge species which filter FPOM (fine particulate organic matter) from the passing water. Also, certain species of mayflies, midges, oligochaetes, and amphipods (may also function as shredders) gather particles from the sediments. Grazers or scrapers include certain species of caddisflies, mayflies, snails, and beetles. In addition to the fish shown at the left, the major predators are hellgrammites, dragonflies, tanypod midges, and certain species of stoneflies. The midregion of the river system is seen as the major zone of plant growth (algae, or periphyton, and rooted vascular plants) where the ratio of gross primary production (P) to community respiration (R) is greater than 1. Fish populations grade from invertebrate eaters in the headwaters to fish and benthic invertebrate eaters in the midreaches to benthic invertebrate and plankton feeders in the large rivers. (Modified from Cummins 1975).

FOOD BASE AND BIOLOGY OF FORESTED STREAMS

The food base for the biological communities of forest streams consists of leaves, needles, cones, twigs, wood, and bark. The large boles which help shape the small stream are usually biologically processed in place. The input of bole material to the stream is not a regular annual occurrence. Leaves, cones, twigs, lichens, and other components of fine litter have a reasonably predictable timing of input to and export from streams. Of the organic material which falls or slides into first-order streams every year, only 18-35 percent may be flushed downstream to higher order streams. These streams are very retentive, not mere conduits exporting materials quickly to the sea. Sixty to 70 percent of the annual organic inputs are retained long enough to be biologically utilized by stream organisms. Big wood debris dams serve as effective retention devices for fine organic material, allowing time for microbial colonization and insect consumption of this material. Functionally the invertebrates of streams flowing through forests have evolved to gouge, shred, and scrape wood and leaves and to gather the fine organic matter derived from breakdown of coarser material (Cummins 1974; Anderson et al. in press).

Woody debris and leaves, the two major allochthonous components entering a stream from the riparian zone, operate in different ways in relation to quantity, quality, and turnover time of standing crop. The leaves form a small pool of readily available organic material, while the wood forms a large pool of less available organic matter. The slowly processed wood also constitutes a long term reserve of essential nutrients and energy. The composition, metabolic structure, and nutrient turnover time of the particulate organic pool effectively provide both flexibility and stability within the system.

The amount of debris processed in a defined reach of stream depends on two factors: (1) the nature of the debris (abundance and species of wood or leaves) and (2) the capacity of the stream to retain finely divided debris for the period of time required to complete processing. Debris undergoing utilization by stream biota may either be utilized fully within a stream reach or be exported to a downstream reach. Processing continues as small debris moves along the drainage because export from one reach constitutes downstream input. Processing includes both material used metabolically by bacteria and fungi and those debris pieces physically abraded by mineral sediment or by insect consumption. In all cases, the debris is broken into smaller pieces which increases the surface-to-volume ratio and makes a debris particle increasingly susceptible to microbial attack.

Wood in streams is a substrate for biological activity and it creates other habitat opportunities by regulating the movement of water and sediment. To measure the importance of large organic debris from the riparian zone in streams, Swanson and Lienkaemper (unpublished data) examined several streams and measured percent of stream area in (1) wood, (2) wood-created habitat, principally depositional pools, and (3) nonwood habitat such as bedrock and boulder cascades. In a 245-m section of Mack Creek, a third-order stream flowing through an old-growth Douglas-fir stand in the western Cascade Range, Oregon, 11 percent of the stream area is in wood, 16 percent in wood-created habitat, and 73 percent in nonwood habitat. Figure 4 shows an example of the distribution and quantity of debris in a section of Mack Creek. In a first-order tributary draining 10 ha, wood comprises 25 percent of the stream area and another 21 percent is habitat created by wood. Much of the biological activity by detritus-processing and consumer organisms is concentrated in the areas of wood and wood-created habitat. Each habitat type has a different faunal composition.

Wood Habitat Community

Wood habitat communities are distinctive. The primary utilizers are beetles, midges, and snails. In addition to the food supplied to the major wood eaters, the surface area and large number of protective niches on wood afford considerable living space and concealment. Wood is used for oviposition, as a nursery area for early instars, for resting, molting, pupation, and emergence. Because of its unique capillary properties, it affords an ideal air-water interface where gradients of temperature and moisture can be selected by different taxa for various activities.

Wood-Created Habitat

The depositional areas behind large debris are prime areas for processing leaf material and the fine organic matter derived from wood. These areas are richer than the wood habitat community both in numbers and biomass of invertebrates. Leaves and the shredders (primarily caddis- and craneflies) are concentrated in these areas. Many of the shredders feeding here will use the wood habitat to molt, pupate, and emerge.

The difference in invertebrate biomass on leaves and wood is attributed primarily to differences in food quality. Although both are low in nitrogen compared with periphyton, seeds, or fresh macrophytes, the wood is so high in the refractory components lignin and cellulose that it becomes available at a very slow rate. The greater surface area and penetrability of leaves results in microbial con-

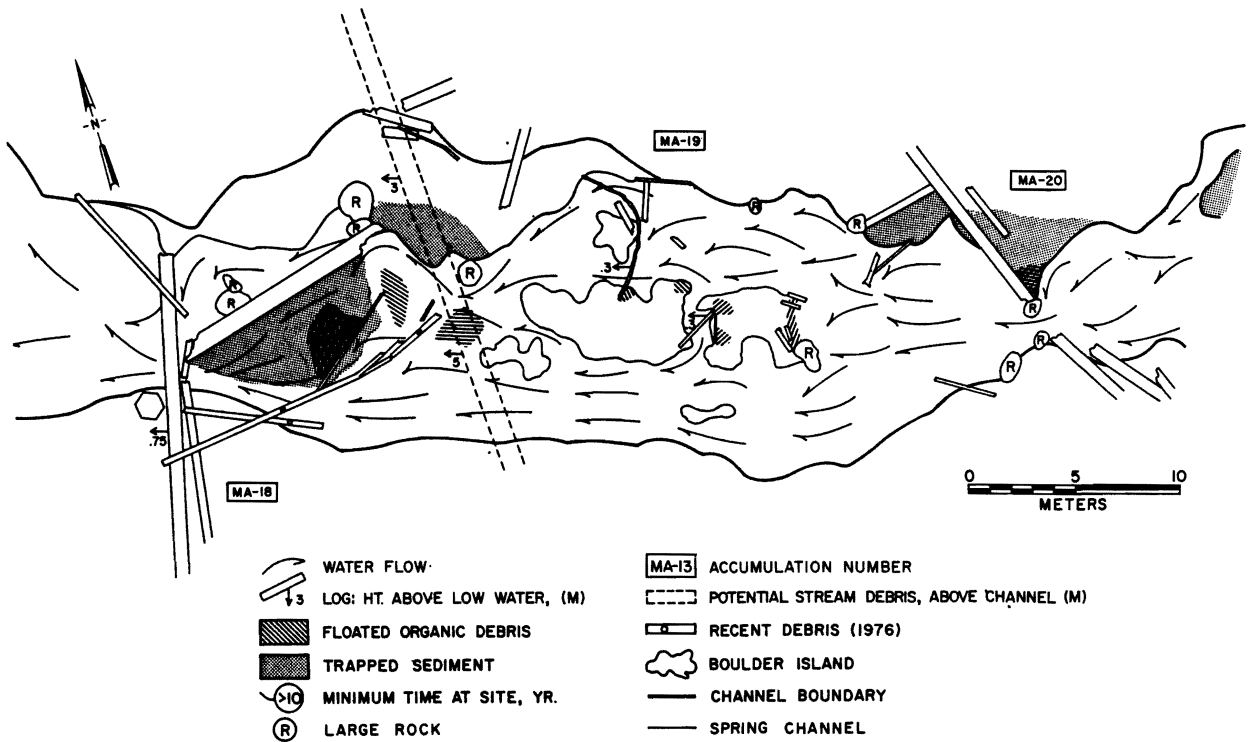


Figure 4.--Distribution of debris in a section of Mack Creek, western Oregon. Courtesy of George W. Lienkaemper.

ditioning occurring within months, compared with years for wood. Conditioning is a key factor in the debris becoming available as food for the invertebrates.

RELATIONSHIP OF RIPARIAN VEGETATION TO SALMONIDS

Direct Influences

The previous discussion has described how riparian vegetation contributes to primary stream productivity through input of organic material and nutrients which are utilized by various components of the stream biota. These relationships directly affect the production of fish by establishing the basic components of the food chain which eventually lead to the fish themselves. Likewise, necessary portions of salmonid habitat are created by large pieces of debris from the riparian zone. Logs and debris jams create pools and protective cover. This type of habitat also provides communities of benthic organisms different from those associated with the shallower and faster waters of riffles and runs. This increase in diversity of invertebrates provides a more useable food base for the fishes, which depend to a great extent upon them. A large part of the diet of fish in the family Salmonidae (the various Pacific salmon, trout, and char) is aquatic insects and other invertebrate organisms.

Indirect Influences

In addition to the effect of riparian zone material which directly becomes a part of the stream system, streamside vegetation has many important indirect influences on the habitat of salmonids.

Water Temperature

The principal source of heat which raises water temperatures is direct solar radiation (Brown 1969). Consequently, streamside vegetation is important in maintaining water temperatures suitable for spawning, egg and fry incubation, and rearing of anadromous and resident salmonids. Several studies in the last decade have demonstrated how streamside vegetation directly controls water temperature (Levno and Rothacher 1967, Brown and Krygier 1970, Meehan 1970, Burns 1972). The literature is also rich with documentation of the effects of streamside canopy removal on stream temperatures (Hall and Lantz 1969, Meehan et al. 1969, Brown and Krygier 1970, Burns 1972, Moring 1975).

Stream temperature is directly proportional to surface area and solar energy input, and inversely proportional to streamflow (Gibbons and Salo 1973). Therefore, small forested streams are the most susceptible to temperature

change. The insulating effect of riparian vegetation is thus of primary importance in maintaining acceptable stream temperatures in the many small streams which cumulatively produce a significant portion of the salmon and trout populations of the Western United States.

Sediment

Another major function of riparian vegetation is to act as a buffer or "filter" against sediment and debris which would otherwise be deposited in the stream. Surface runoff is a primary vehicle for the transportation of sediment to streams from adjacent sources, either natural or man-created. The herbaceous communities within the riparian zone are effective in reducing the impacts of this runoff, and the larger shrubs and trees prevent larger debris from entering the stream channel. The value of streamside vegetation for stream protection has been quantified in economic terms by Everest (1975).

Sediment which affects salmonids occurs in two general forms. As suspended sediment, it can be harmful if concentrations are high and persistent (Cordone and Kelley 1961). Under these conditions, silt may accumulate on the gill filaments and actually inhibit the ability of the gills to aerate the blood, eventually causing death by anoxemia and carbon dioxide retention.

Bedload sediment, however, probably limits salmonid production more than suspended sediment. Excessive deposited sediment reduces the flow of intragravel water, which in turn limits the supply of oxygen available to incubating eggs and alevins, and hinders the removal of metabolic waste products (Sheridan 1962, Vaux 1962, Cooper 1965, McNeil 1966). Bedload sediment may also act as a physical barrier, preventing the emergence of newly hatched fry up through the gravel (Koski 1966, Fall and Lantz 1969).

Another effect of sediment is the alteration of habitat used by aquatic insects (Wagner 1959) which directly relates to the growth and condition of the fish which utilize them. Although biomass may not decrease, the species composition may change such that the new forms are not as readily available to the fish.

Cover

The extensive rooting of herbaceous riparian vegetation aids in streambank stabilization. As a result, where streamside vegetation is intact, the occurrence of undercut banks is higher. This is prime habitat for trout and young salmon. Overhanging streamside vegeta-

tion also acts as escape cover and in some instances as a deterrent against predation by birds and mammals.

Insects

As discussed earlier, riparian vegetation contributes to the food base of stream biological communities in the form of wood and other organic debris. In addition, streamside vegetation is important in directly providing insects to the stream which then become part of the available fish food. Terrestrial insects which are associated with the various strata of the riparian zone become "accidental" fish food items. Many of the aquatic insects use streamside vegetation during emergence and in the adult stages of their life cycle.

EFFECTS OF LAND USE PRACTICES

Many of man's activities affect the riparian zone to varying degrees. We must consider logging and road construction to be among the most severe disturbances. Until recently it was common practice to clearcut timber to the stream's edge. In addition to removing the trees which provided shade to the stream surface, the understory vegetation and ground cover were usually cut down or severely disturbed. In recent years, the importance of the smaller streams has been more fully recognized and buffer strips along streams are often left.

The riparian zone is also affected by livestock grazing. In addition to cropping off much of the herbaceous vegetation along streambanks, livestock also use the smaller shrubs and young trees as forage. As a result, much of the ground cover and many of the plants which provide shade to small streams are removed. The soil along the streams is compacted by trampling, and together with the removal of the "filtering" plants a situation is created which promotes the addition of fine sediment to the streams. Wild ungulates also utilize the riparian zone, but their presence is much less noticeable than that of cattle and sheep. A workshop was conducted in Reno in May 1977 to bring together existing knowledge on the relationships between livestock and fisheries, wildlife, and range resources. A large part of the material which was discussed at this workshop concerned the riparian zone, and will soon be available.⁴

⁴USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California (in press).

SUMMARY

The riparian zone is a very important area influencing the habitat of salmonids. Much of the wood which forms the food base for stream biota comes from the riparian zone. This same wood, when it falls or slides into a stream, has an important role in shaping the stream and creating its habitat types. Streamside vegetation provides shade to the stream surface, thereby maintaining water temperatures acceptable to salmonid fishes. The roots of woody and herbaceous plants provide streambank stability and help to create overhanging banks, an important component of salmonid habitat. Streamside vegetation provides habitat for the later life history stages of aquatic insects and for terrestrial insects which accidentally become part of the food utilized by salmonids.

When the riparian zone is affected by man's activities, the quality of fish habitat will likewise be affected.

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