CHAPTER 10

ROLE OF ANAEROBIC ZONES AND PROCESSES
IN STREAM ECOSYSTEM PRODUCTIVITY

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ABSTRACT

The character of flowing waters in North America has changed
dramatically since the days of early exploration and colonization.
Channel complexity, debris accumulations, beaver activity, riparian
vegetation, and the extent and structural diversity of the
floodplain have often been greatly reduced. These features all
affect the ability of a stream or river to trap, retain, and store
organic materials. Historically, accumulations of organic matter
that resulted in anaerobic interstitial waters were widespread and
commonplace in streams. Concentrations of ammonia, organic
nitrogen, organic carbon, organic phosphorus, phosphate, and
numerous metals are much greater within these zones. These regions
of the sediment represent important areas of nutrient regeneration
and potential sites of eventual nutrient introduction into stream
waters. The overall productivity of stream ecosystems is enhanced
by the greater nutrient availability represented by these regions
where anaerobic processes occur and nutrients are recycled into
soluble, mobile forms.

INTRODUCTION

Rivers and streams have served as magnets for colonization and
utilization throughout history. Available water, rich soils, wood,
grazing areas, and a source of transportation have drawn people to
their banks and riparian zones. The exploration and settlement of
the Americas by Europeans followed major waterways. Human activity
remains concentrated in these areas (Tiner, 1984).

Industrialized society has developed numerous methods and machines that enable people to fundamentally alter the shape, form, and functioning of streams and rivers. In North America, these various impacts can be traced back as far as initial exploration and settlement. Few if any streams or rivers in the United States have remained totally untouched (Sedell and Luchessa, 1982).

Almost without exception, the first impact of Europeans on North American streams and rivers involved fur trappers. Beavers, in particular, were a major impetus for exploration and a major economic boon to the New World. Throughout the United States, the first European explorers were inevitably trappers. The exploitation of the resource was intense. Seton (1929) estimated that primal beaver populations in North America ranged from between 60 and 400 million or between 6 and 40 animals for each km of stream and river. Recent estimates place modern populations at 1 to 2 million animals, or approximately 0.1 to 0.2 animals per km (Denney, 1952).

The overall impact on floodplain landscapes has been substantial if one considers that populations of the prime animal agent of geomorphic change have been reduced one to two orders of magnitude. For example, Dobyns (1981) has suggested that arroyo formation, stream incision and increased flooding followed closely on the heels of beaver removal with subsequent dam failure and cattle introduction in the Gila River drainage of New Mexico. These features have been accepted for many years as ones natural to floodplain landscapes in the arid west. The diaries and reports of the early trappers, however, repeatedly record waters rich with beavers, lush with riparian vegetation, and running clear and cold where now they are channelized, silt-laden, and intermittent (Loyola, 1939; Cleland, 1950; Hastings and Turner, 1965; Weber, 1971; Dobyns, 1981). Beavers, a key geomorphic agent in streams and rivers, were greatly reduced in number throughout the United States at least a century ago.

A second widespread impact of human beings on streams and rivers began once permanent settlements were established. Waterways were a primary means to transport and market the agricultural output and natural resources of a region. Sedell and Luchessa (1982) documented the clearing of snags, boulders, and debris dams from almost every region of the United States. For more than a century, large wood and other obstructions have been systematically removed from rivers and streams (see Reports of the Secretary of War, Chief of Engineers, 1875 to 1914, for a detailed account of locations, maps, and numbers of logs removed). As one example, Triska (1984) has carefully documented the historical role of wood debris on a 400 to 500 km stretch of the Red River, Louisiana. Wood debris choked the channel. Exposed wood covered 80 to 120 km of channel and in one area 225 km of channel were affected. After 70 yr of intense channel and riparian zone clearing, a wide, unobstructed, meandering channel was produced by 1904. Today, this morphology may mistakenly be viewed as typical of pristine lowland rivers. Sedell and Froggatt (1984) have similarly reconstructed the historical changes to the Willamette River, Oregon. From 1870 to 1950, over 58,500 snags and streamside trees were pulled from a 114 km reach of the river. A pristine riparian forest originally

extended 1.5 to 3.0 km on either side of the main channel. Now, after 80 yr of intense activity within the riparian zone, there exists one channel, few downed trees and a four-fold decrease in shoreline length. The shoals, multiple channels, oxbow lakes, and extensive marshes, wetland, sloughs, and backwaters are gone. Similar scenarios during the same time period can be documented in lotic ecosystems throughout North America.

A third impact of major historical importance was the introduction of domestic grazers to riparian ecosystems. Livestock commonly concentrate their foraging and calving near streams. In more xeric climates the end result of heavy grazing pressure is often the change from perennial to intermittent flow (Winegar, 1977; Stabler, 1985). Arroyo cutting, increased sediment loads, and channel incision often result (Dobyns, 1981). Most of the public lands of the western United States have been managed now for nearly a century as areas for livestock production. The riparian vegetation, channel geomorphology, hydrology, and stream processes have adjusted in numerous ways to the increased utilization by domestic animals.

Fourth, the use of rich alluvial soils for agriculture and the building of homes on the floodplain demanded a massive effort to control the course and quantity of flow in streams and rivers. Channelization and the building of levees, dikes, revetments and dams have attempted to restrict flow into well-defined main channels and irrigation ditches. Flood control has released vast areas of the floodplain for development of farmlands and cities. Containment of even the smallest of streams is now routinely practiced for irrigation, flood control, and livestock watering. Many of the lotic ecosystems of North America are now carefully regulated and are not representative of conditions under which native riparian vegetation and stream and river processes evolved (Fenner et al., 1985; Bradley and Smith, 1986).

Finally, the depression of the 1930's helped to further imprint human activities on many of the most remote and undisturbed streams remaining in the United States. Works Progress Administration and Civilian Conservation Corps crews participated in massive "clean up" efforts designed to remove large debris accumulations from streams throughout the United States (Sedell and Luchessa, 1982). The Federal Flood Control Act of 1936 made funds available for the clearing of almost any size stream anywhere in the United States. Debris dams, snags and brush were fastidiously removed. Thousands of miles of stream channel were made open and unobstructed.

Historical records help to reconstruct the primal conditions of riparian zones and streams. Two common themes reverberate throughout these records: 1) streams today are generally less retentive of organic matter and 2) riparian and stream ecosystem interactions have been widely uncoupled. Whether the focus is on beaver trapping, channel clearing, flood control, grazing, agricultural activity, or urbanization, human influence has acted to reduce long-term retention and storage of organic and inorganic material within the stream and floodplain and to diminish the extent of interaction between the riparian zone and the channel. A dynamic, heterogenous landscape has been increasingly molded into a more static, homogeneous one by human forces.

There are several reasons we stress the importance of historic reconstruction in studying stream-riparian interactions. First, Margalef (1960) proposed that the successional stage of a given terrestrial ecosystem determined the successional stage of a segment of stream flowing through it. This concept suggests a discontinuous series of stream habitats making up a waterway. The river continuum hypothesis (Vannote et al., 1980) and its refinement (Minshall et al., 1983) suggest that there are continuous gradients of structure and function from headwaters to mouth in a river system. Both ideas necessarily have, to some extent, been based on the structure and function of present-day stream and riparian systems. To understand underlying relationships in the floodplain between stream and riparian systems, it is instructive to know the historical backdrop upon which the present conditions came to exist. Sedell and Froggatt (1984) pointed out that even on major rivers there historically was extensive morphological heterogeneity produced by large quantities of woody debris. Within a large floodplain there would be much exchange between stream and riparian vegetation. Also, picture frequent positional changes of geomorphic surfaces, numerous types of channels (narrow or broad), and a variety of flow characteristics-- stagnant to free flowing. This is a profoundly different landscape from present-day floodplains and has important implications for the development of any theory concerning continua or discontinua of structure and function, and stream-riparian exchange.

Second, nutrient-spiralling theory (Elwood et al., 1983; Newbold et al., 1982) states that where there are mechanisms of retention, then the nutrient spirals become tighter; if there are few mechanisms enhancing retention, then the nutrient spirals grow longer. According to the river continuum hypothesis, large woody debris is an important structural component in headwater streams, but diminishes in importance in larger streams. Would spiralling length as a result then be shorter in headwater streams than in larger streams? The historical research of Sedell and Froggatt (1984) argues against making such predictions concerning the role of woody debris or spiralling length based on stream order.

Third, Hynes (1983) and Grimm and Fisher (1984) have pointed out the importance of interstitial waters as source areas for organic matter and key regions of stream metabolism and nutrient cycling. Hynes (1983) forcefully emphasized our lack of knowledge about conditions in the hyporheic zones of streams, drawing attention to the interstitial portion of the stream and the chemical and biological processes occurring there. Grimm and Fisher (1984) showed that a seemingly autotrophic desert stream was actually heterotrophic when metabolism within the sediment and interstitial waters was included in the estimates of stream respiration. Historical research suggests that conditions which would promote interaction and exchange between the stream and the interstitial waters of the sediment and riparian soils have been systematically removed or reduced throughout North America.

In summary, historic reconstructions repeatedly show that the floodplain landscapes of both small and large river systems were more complex and heterogeneous in space and time than they are presently. Redistribution of energy and nutrients was frequent and

dependent on physical factors, such as debris dams, and animal agents, such as beaver. It is time to frame riparian-stream interactions in a landscape context. Risser et al. (1984) asked the question, "What formative processes, both historical and present, are responsible for the existing pattern in a landscape?" Efforts to produce a unified theory of stream ecology, research on riparian-stream interactions, and the concept of nutrient spiralling point the way to processes which could have shaped the rich, dynamic mosaic in the historic floodplain landscape.

The purpose of this paper is to present data on interstitial nutrient chemistry from anaerobic zones of stream sediment where geomorphic and hydrologic processes have created conditions conducive to organic matter accumulation and storage. Such zones, we hypothesize, were much more prevalent in historic floodplains because of the abundance of woody debris and beavers, and the less intense use by human populations. These data will be compared to aerobic interstitial waters and stream water. Also, the biomass of periphyton at the sediment-water interface above these various interstitial zones of the sediment will be compared. Finally, discussion will focus on how geomorphic patterns affect the spatial and temporal distribution of aerobic and anaerobic zones in streams and how these conditions might affect the riparian plant community.

METHODS AND SITES

In this study two sampling sites were used. Sulfur Springs is a second-order stream in the Coast Range of western Oregon. It is a small tributary of Knowles Creek which is a tributary of the Siuslaw River. A debris torrent blocked a portion of the channel and resulted in a section with lower gradient and debris dams. Beavers have occupied the area and have further enhanced the retentive characteristics of the reach. The second site is a reach of the headwaters of the Rio Cebolla in the Jemez Mountains of north-central New Mexico. This third-order stream has historically had extensive beaver activity. The study area includes one of the two remaining beaver colonies on the stream.

Samples for interstitial chemistry were taken with a modified 30-mL syringe. The syringe was marked at 5-cm length and the tip was enlarged to 2-cm diameter. The syringe was inserted into the sediment to a depth of 5 cm and the plunger pulled back to extract a slurry of sediment and water. The sediment and water mixture was immediately placed in sealed centrifuge tubes and centrifuged at 5,000 rpm for 3 min. The liquid supernatant was then decanted into a filtration system and filtered through GF/F filters that had been fired overnight at 450°C. The filtered sample was placed in an ice chest and transported to the lab for analyses. A subsample of 1 mL was also reacted with Ferrozine in the field for subsequent determination of ferrous iron in the lab (Stookey, 1970).

Samples of benthic algae were collected using a circular cork borer with a 2.5-cm diameter. Total chlorophyll was measured using the method of Parsons et al. (1984). Organic carbon content of the sediment below the algal mats was determined by ashing at 550°C for 4 hr and measuring weight loss.

Nitrate, ammonia, and phosphate were measured using automated nutrient analysis as described by Strickland and Parsons (1972). Dissolved organic nitrogen was calculated by subtracting the ammonia concentration from the Kjeldahl nitrogen value. Kjeldahl nitrogen was determined by automated ammonia analysis after sample digestion (Strickland and Parsons, 1972). Total phosphorus was measured as phosphate by automated nutrient analysis following persulfate and sulfuric acid digestion (Rand, 1976). Dissolved organic carbon (DOC) was measured as CO_2 after persulfate oxidation using the method of Menzel and Vaccaro (1964). Methane was measured using gas chromatography following the procedure of Lilley et al. (1983).

RESULTS

Comparisons of nutrient concentrations in anaerobic and aerobic zones of interstitial water were made at six sites in Sulfur Creek, Oregon. In addition, stream water samples were taken immediately above the interstitial samples at each site. Of the six interstitial waters samples, three were aerobic and three were anaerobic. Anaerobic samples occurred in the sediments of ponds behind debris dams or beaver dams. Aerobic samples were found at 5 cm depth in pools either upstream or downstream of the debris and beaver dams and in sediments immediately downstream of one of the debris dams in a free-flowing reach of stream.

Concentrations of ammonia, nitrate, and dissolved organic nitrogen (DON) are listed in Table 1. The reduced forms of nitrogen, ammonia and DON were present in higher concentrations within the anaerobic interstitial waters. Average ammonia values were 1.887 mg/L in the anaerobic samples, 0.334 mg/L in the aerobic samples and 0.023 mg/L in the stream water. Average DON values were were 4.014 mg/L in the anaerobic samples, 1.279 mg/L in the aerobic samples and 0.116 mg/L in the stream water. Interstitial waters collected in these various depositional environments were routinely at least one order of magnitude above stream values for ammonia and DON. Anaerobic zones had the highest levels of ammonia and DON. Going from the stream water to anaerobic interstitial waters at 5-cm depth in the sediment, a two orders of magnitude increase sometimes occurred. Nitrate concentrations showed the reverse trend. Average nitrate concentrations were 0.014 mg/L in the anaerobic samples, 0.058 mg/L in the aerobic samples and 0.100 mg/L in the stream water.

Dissolved organic carbon (DOC) and methane concentrations at the Sulfur Springs sites are given in Table 2. The average concentration of DOC was 37.7 mg/L as carbon for the anaerobic samples, 12.5 mg/L for the aerobic samples, and 1.8 mg/L for the stream water. A strong gradient existed between the stream water and the interstitial waters, particularly in or near the anaerobic zones. Methane samples were collected from the water immediately above the sediment-water interface. Substantial methanogenesis was occurring in the anaerobic regions of interstitial water as seen by the highly supersaturated levels of methane in waters in the very

retentive reach of the stream. Average methane values were 0.278 mg/L in these waters compared to 0.005 mg/L in the water in pools upstream and downstream of the debris and beaver dams.

Table 1. Oxygen Conditions and Nutrient Concentrations in mg/L for Ammonia, Nitrate, and Dissolved Organic Nitrogen in the Stream and Interstitial Waters of Sulfur Creek, Oregon.

Site	O_2[1]	NH_4	NO_3	DON
Upstream pool	Aerobic	0.275	0.125	0.813
Upper debris dam pond	Anaerobic	1.100	0.030	2.363
Lower debris dam pond	Anaerobic	4.100	0.013	6.000
Immediately below debris dam	Aerobic	0.413	0.000	2.175
Old pond	Anaerobic	0.460	0.000	3.680
Downstream pool	Aerobic	0.313	0.050	0.850
Stream water[2]	Aerobic	0.023	0.100	0.116

[1]Based on the presence or absence of ferrous iron.
[2]Composite of six samples from above the six sites where interstitial waters were collected.

Table 2. Oxygen Conditions and Nutrient Concentrations in mg/L for DOC and Methane in the Stream and Interstitial Waters of Sulfur Creek, Oregon.

Site	O_2[1]	DOC	CH_4[2]
Upstream pool	Aerobic	8.2	0.002
Upper debris dam pond	Anaerobic	17.0	0.387
Lower debris dam pond	Anaerobic	82.6	0.320
Immediately below debris dam	Aerobic	20.6	0.128
Old pond	Anaerobic	13.4	-
Downstream pool	Aerobic	8.8	0.008
Stream water[3]	Aerobic	1.8	-

[1]Based on the presence or absence of ferrous iron.
[2]Methane samples were collected just above the sediment-water interface and not from the interstitial zone.
[3]Composite of six samples from above the six sites where interstitial waters were collected.

Phosphorus concentrations, both as phosphate and total phosphorus, were also much higher in interstitial water than stream water (Table 3). Phosphate levels averaged 0.638 mg/L in the anaerobic samples, 0.467 mg/L in the aerobic samples, and 0.007 mg/L in the stream water. Total average phosphorus concentrations were 0.792 mg/L in the anaerobic waters, 0.642 mg/L in the aerobic waters, and 0.026 mg/L in the stream water. Increases of one order of magnitude in concentration commonly occurred for phosphate and total phosphorus between stream water and interstitial waters in depositional areas of the stream. The differences in concentration between the aerobic and anaerobic zones were proportionally smaller for phosphate and total phosphorus than for DOC, ammonia, and DON. All interstitial waters, however, were greatly enriched over stream levels for both phosphate and total phosphorus. Abundant accumulations of benthic algae were often noted in stream reaches with extensive debris accumulations, beaver activity, and large amounts of organic matter storage. Stream reaches in these areas which were well-lit had especially large mats of benthic algae. Sampling was carried out in the Rio Cebolla, a meadow stream with beaver ponds, to quantify the amount of chlorophyll in various reaches (Table 4). Samples were collected from the reach immediately downstream of a beaver dam (less than 10 m below), the edges of the beaver pond, and upstream of the pond (10 m upstream). Sediments at 5 cm depth throughout the pond were anaerobic. The chlorophyll values showed a striking pattern with approximately a ten-fold increase from above the pond to within the pond. In the reach immediately below the pond, the chlorophyll levels were nearly 20 times those in the upstream reach.

Table 3. Oxygen Conditions and Nutrient Concentrations in mg/L for Phosphate, and Total Phosphorus in the Stream and Interstitial Waters of Sulfur Creek, Oregon.

Site	O_2[1]	PO_4	TP
Upstream pool	Aerobic	0.350	0.563
Upper debris dam pond	Anaerobic	0.375	0.475
Lower debris dam pond	Anaerobic	0.820	1.000
Immediately below debris dam	Aerobic	0.600	0.863
Old pond	Anaerobic	0.720	0.900
Downstream pool	Aerobic	0.450	0.500
Stream water[2]	Aerobic	0.007	0.026

[1]Based on the presence or absence of ferrous iron.
[2]Composite of six samples from above the six sites where interstitial waters were collected.

Table 4. Sediment Organic Content (%) and Total Chlorophyll
(µg/cm²) from above, in, and below a Beaver Pond in
the Rio Cebolla, New Mexico.

Site	n	Sediment organic content (%)	Total chlorphyll (µg/cm²)
Above pond	3	2.6 +- 2.0	0.79 +- 0.24
In pond	4	7.6 +- 2.4	7.35 +- 3.27
Below pond	2	5.5 +- 0.1	14.64 +- 1.37

DISCUSSION

Historical research presents a long-term perspective from which
to begin to consider the temporal and spatial heterogeneity of
streams and riparian zones. The changing mosaic along streams
provides a template on which various processes occur and different
biotic communities are distributed. How do the important roles of
large organic debris, beaver activity, complex channel morphology,
and enhanced retention and storage of organic detritus affect
stream processes and the plant community of the riparian zone?

An important effect is the ability of the stream to retain,
store, and process organic inputs. Efficient retention of organic
inputs not only influences the quantity of organic matter available
but can also dictate the pathway by which much of this material is
decomposed. Anaerobic decomposition occurs when oxygen
availability does not meet the metabolic demands of the decomposer
population. Reaches of stream with debris dams, beaver ponds,
sloughs, backwaters, and side channels create areas where
widespread anaerobic conditions potentially can occur within the
interstitial sediments. Anaerobic sediments are more likely to
exist where accumulations of organic material and fine-grained
sediments occur in regions of relatively restricted exchange
between surface and interstitial waters. The extent to which this
type of environment is found in streams has not been investigated,
but the data presented in this paper show that nutrient concentra-
tions, the chemical form of various nutrients, and the rate and
pathways of nutrient cycling can be shifted dramatically in these
environments (Tables 1-3). The overall extent of anaerobic
interstitial waters will be closely linked to physical, hydrologic,
and geomorphic process within each drainage.

Light, nitrogen, and phosphorus are common factors limiting the
rate of primary production in streams (Peterson et al., 1983;
Gregory, 1980; Elwood et al., 1983; Triska et al., 1983; Grimm and
Fisher, 1986). The structure of the riparian zone strongly in-
fluences the amount of light reaching the stream. Primary produc-
tion in highly-shaded streams is commonly light-limited (Gregory,
1980). Where shading becomes less of a problem, a nitrogen or
phosphorus limitation often is present (Peterson et al., 1983;
Grimm and Fisher, 1986). Anaerobic interstitial waters are greatly

enriched in both nitrogen and phosphorus when compared to the overlying water of the stream (Tables 1 and 3). The gradient between the aerobic sediment-water interface and the anaerobic zone supports a flux of nitrogen and phosphorus to the interface. The predicted response would be increased rates of primary production in these zones where light is not a limiting factor. In many ways, this response would be similar to stream enrichment experiments where direct addition of nutrients to the stream stimulates increased photosynthetic activity and standing crops from the periphyton community (Gregory, 1980; Triska et al., 1983; Elwood et al., 1983; Petersen et al., 1983; Grimm and Fisher, 1986). The difference is that the increased supply of nutrients is supported by anaerobic processing within certain zones of the stream sediments and floodplain, which are then mobilized to the benthic algal community by turbulent diffusion and the concentration gradient which arises. The standing crop of algae indicated by the total chlorophyll data (Table 4) supports this scenario, but direct measurements of the rates of primary production would be a better test.

Changing conditions of oxygen and nutrient concentrations may also be key variables influencing the structure and composition of the riparian plant community. Increased nutrient concentrations and changes in chemical forms and ratios in anaerobic zones and around aerobic-anaerobic interfaces present both potentially advantageous and deleterious conditions for various plants. What effects do increased concentrations of ammonia, DON, DOC, and phosphorus, but low concentrations of nitrate and oxygen, have on the riparian plant community?

Until recently, most research on riparian-stream interactions has focused on contributions from plants to the stream. Large organic debris (Bilby, 1981; Cummins, 1980; Keller and Swanson, 1979; Keller and Tally, 1979; Sedell and Froggatt, 1984; Swanson et al., 1982; Triska, 1984; and Triska et al., 1982), plant nutrient contribution to stream nutrient economy (Bormann and Likens, 1967; Elwood et al., 1983; Minshall, 1978; Petersen and Cummins, 1974), stream retention of organic inputs (Speaker et al., 1984), shading and buffering roles of riparian vegetation (Aho, 1976; Brown and Kryger, 1970; Gray and Edington, 1969; Lowrance et al., 1984a; Nabhan, 1985), reclamation of ephemeral streams (Heede, 1981), and the relationship of terrestrial and stream succession (Fisher, 1983; Margalef, 1960; Molles, 1982; Vannote et al., 1980) have been considered.

Recently, however, the effects of stream hydrology and geomorphology on riparian plant community composition and distribution have become an active arena for research. Floods and stream meandering create geomorphic surfaces such as sand and gravel bars, swales and natural levees which, in part, determine plant species distribution on the floodplain (McKee and Swanson, personal communication; Hupp and Ostercamp, 1985). These geomorphic surfaces also establish the template upon which nutrient dynamics and oxygen utilization and resupply are superimposed. A number of possible responses can be hypothesized to occur within the riparian plant community to this mosaic of geomorphic surfaces, oxygen availability, and nutrient dynamics. For example, oxygen

levels in the soils and sediments may be an important variable in structuring riparian plant communities with their ability to handle various periods of anoxia as a determining role in plant distributions (e.g. Crawford, 1966). Nutrient chemical form and cycling rates may also be key elements in the structure and composition of the riparian plant community, although limited research in these veins has yet been reported. Possible responses of riparian plants to changing nutrient conditions associated with anaerobic zones or near aerobic-anaerobic interfaces that deserve consideration include: 1) total nitrogen and phosphorus content within the plant; 2) the nitrogen to phosphorus ratio within the vegetation; 3) plant allocation of photosynthate to either vegetative growth or sexual reproduction; 4) changes in phenology with different nutrient levels or ratios; and 5) compensatory ability of the plant to respond to herbivory. These possible responses to shifts in the form and concentration of plant nutrients may also influence the structure and composition of plants in the riparian zone.

Many riparian plants are anatomically and physiologically adapted to withstand low O_2 conditions found in saturated soils. Anatomical adaptations in many woody riparian species include well-developed stem lenticels which allow them to grow in low O_2 conditions (Koslowski, 1984). Air moves through the lenticels by diffusion to root aerenchyma, and toxic products of respiration are volatilized and released via the lenticels (Chirkova and Gutman, 1971; Hook and Scholtens, 1978). Many flood-adapted species are extremely sensitive to anoxia (Koslowski, 1984) but the well-developed aerenchyma-lenticel system insures an oxygen supply to roots growing in anaerobic conditions. Riparian plants are also adapted physiologically to varying periods of flooding or anoxia. Some species resistant to O_2 deficiency such as *Salix alba* can decrease respiration rates and detoxify metabolic products by volatilization, root exudation, or secondary metabolism (Chirkova, 1978). McMannon and Crawford (1971) showed an inverse relationship between flood tolerance and production of alcohol dehydrogenase in roots. Armstrong (1975, 1978) reported that although sensitive to anoxia, roots of wetland plants growing in permanently anaerobic soils maintained a fairly steep O_2 gradient from lenticel to root meristem, where respiration requires much O_2. Armstrong (1971) and Hook et al. (1971) showed that roots actually leak O_2 to the rhizosphere. Therefore, two processes, respiration and root exudation of O_2, maintain the O_2 gradient necessary for survival in anaerobic soil. Oxygen leakage into the rhizosphere could confer at least three advantages on plants. First, oxidation of the rhizosphere creates a nutrient-rich aerobic-anaerobic interface at the site of mineral nutrient uptake. Second, oxygen stimulates the activity of nitrogen-fixing bacteria and fungal symbionts (Armstrong, 1978), and third, stimulation of mycorrhizae may lead to increased NH_4^+ (Rygiewicz et al., 1984), the form of inorganic nitrogen most abundant in reducing environments (see Table 1). Another physiological adaptation to flooding is the rapid production of adventitious roots above the anaerobic zone (Koslowski, 1984). The placement of these roots may enable plants to take advantage of the

nutrient enrichment occurring near anoxic interstitial water. Riparian plants clearly possess anatomical and physiological adaptations to overcome low dissolved O_2 concentrations.

Riparian plants can use nutrient supplies in the interstitial waters of the riparian zone. Asmussen et al. (1979) showed that NO_3N streamflow outputs from fertilized row-crops were much less after passing through the riparian zone. They concluded that NO_3^- uptake within the riparian zone between the field and stream was responsible. Lowrance et al. (1984b) showed that riparian plants were highly retentive of N and moderately retentive of Ca, P and Mg.

Nutrient distributions in the riparian zone can also affect growth rate, species representation, distribution, and reproduction. Woody species such as willow (Salix sp.) use both nitrate nitrogen and ammonia nitrogen (Smirnoff et al. 1984, W.C. Martin and R.H. Waring, personal communication). Ingestad (1979a, 1979b) showed that concentrations of mineral nutrition in willow tissue varied depending on the rate at which nutrients are supplied. Therefore, willow can track changes in mineral nutrient levels in the soil, and can use ammonia nitrogen as well as nitrate nitrogen. An increase in mineral nutrients favors rapid growth rates. Waring et al. (1985) showed that under different light and nutrient regimes, the leaf chemistry of a willow clone (Salix aquatica) differed. Total N of the high light, high nutrient willows exceeded 5% compared with 1.91% for the high light, moderate nutrient willows. Growth rate was also affected (16.1% per day for high nutrient willows compared with 5.5% for moderate nutrient willows, both under high light). An increase in the N:P ratio available also favors rapid vegetative growth instead of flowering (Salisbury and Ross, 1985; D. Marshall, personal communication). Plants growing in areas of preferential nitrogen enrichment could, therefore, spread very rapidly by vegetative growth. The ability of many woody riparian plants to sprout vigorously when physically damaged by abrasion during a flood may be linked to an abundant nutrient supply. Barnes (1985) attributed the survival of woody riparian species on a frequently flooded island to its ability to spread clonally. Seedling establishment on this island was poor, and clonal growth ensured the spread of established individuals, insuring high immediate fitness (Handel, 1985).

Rapid vegetative growth may also help riparian plants to weather periods of moderate herbivory. Larsson et al. (1986) showed that willow grown under high light and high nutrient conditions had high phenolic glycoside concentrations and were not chosen by defoliating beetles. Belovsky (1981) showed that of two species of birch (Betula sp.), the faster growing one was able to produce more ramets and recovered more rapidly under moose herbivory. Klein (1977) showed that browsing by hare on birch stimulated production of basal shoots, which contain high resin levels and are less preferred than twigs at the top of the tree. Red willow (Salix lasiandra) maintained high growth rates and increased in basal diameter when exposed to beaver herbivory (Kindschy, 1985).
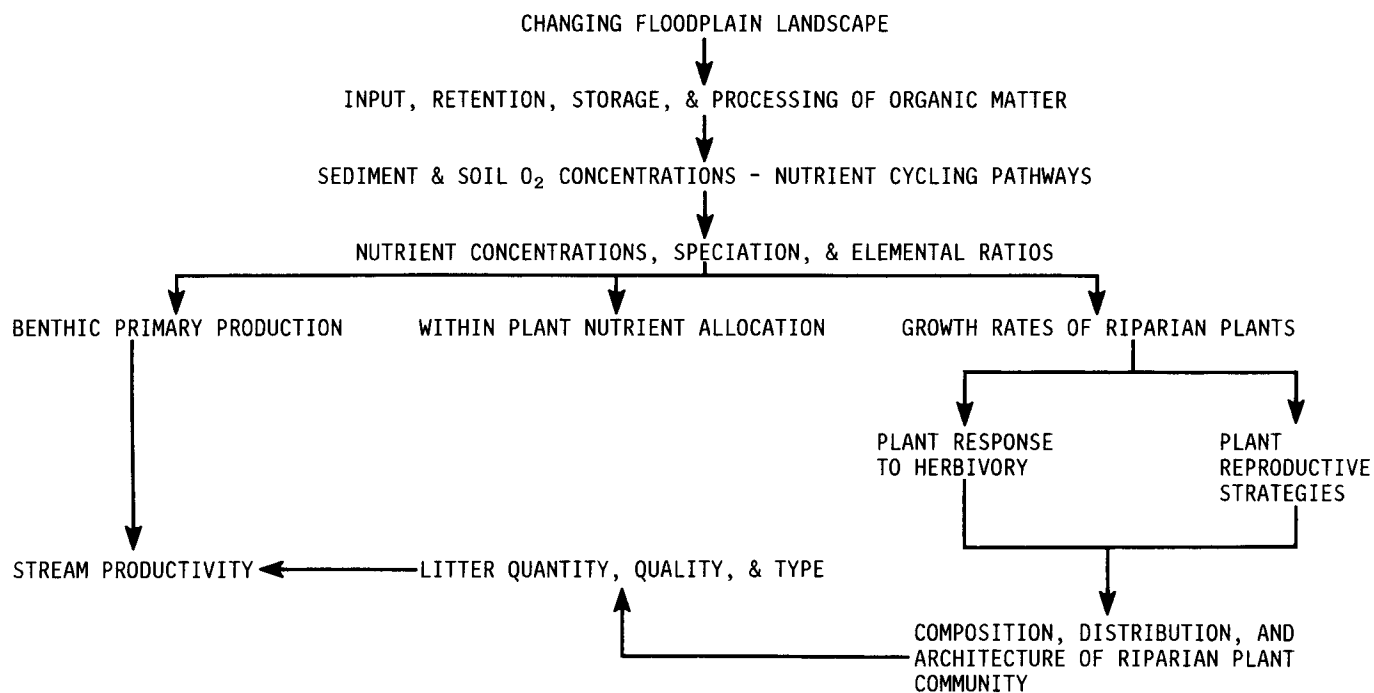
In summary, riparian plants possess anatomical and physiological adaptions to withstand and exploit anaerobic, waterlogged soils. Many of these plants can take up nitrate and ammonia nitrogen and their growth rate is positively correlated with nutrient levels available to them. Therefore, riparian plants may be favored if they tap pockets of nutrient enrichment such as those occurring in the retentive reaches of the two study streams discussed here. Such nutrient uptake potentially affects plant growth rates, clonal spread or sexual reproduction, and response to herbivory. Herbivory might also stimulate changes in plant reproductive strategies by favoring vegetative growth. Changing nutrient conditions and herbivory are largely unstudied forces in determining the riparian plant distribution in floodplain landscapes.

A conceptual model of how changes in the floodplain may affect oxygen distributions, nutrient cycling pathways, and the structure, functioning, and productivity of stream and riparian ecosystems is given in Table 5. Historical changes in the floodplain landscape are predicted to have decreased the input, retention, storage, and processing of energy present as organic matter. This in turn affects dissolved O_2 concentrations within the soil and sediment interstitial waters. Changing oxygen conditions direct nutrient cycling pathways which determine the quantity and type of nutrients present. Nutrient concentrations, chemical speciation, and elemental ratios can potentially help to regulate such processes as benthic primary production, within plant nutrient allocation, and growth rates of riparian plants. These elements of production within the stream and riparian ecosystems can then influence plant response to herbivory, plant reproductive strategies, the composition, distribution, and architecture of the plant community, litter quantity, quality, and type, and overall stream productivity. In general, we hypothesize that highly retentive zones in the floodplains of streams and rivers have been diminished due to protracted and ever-increasing anthropogenic intervention in these areas. Nutrient chemistry, geomorphology, hydrology, and the structure and functioning of streams, rivers, and riparian zones throughout North America are therefore often substantially altered from the primal conditions under which biotic adaptation and evolution once proceeded.

CONCLUSIONS

Anaerobic zones are widespread in retentive reaches of streams where organic matter is efficiently captured, stored, and processed. These regions of the stream and riparian zone are enriched in dissolved ammonia, organic nitrogen, organic carbon, and phosphorus. The historical legacy of ever-increasing anthropogenic utilization of the riparian zone has decreased the amount of large organic debris, the extent of beaver activity, the complexity of riparian habitat, and the diversity of off-channel habitats. Systematic removal of these features has decreased the extent and overall importance of anaerobic pathways of nutrient cycling for numerous riparian areas throughout North America.

Table 5.   A Generalized Conceptual Representation of how Changing Geomorphic Conditions within the
           Floodplain Landscape can Affect Oxygen Concentrations, Nutrient Cycling Pathways, Stream
           Productivity, and the Riparian Plant Community.

CHANGING FLOODPLAIN LANDSCAPE

INPUT, RETENTION, STORAGE, & PROCESSING OF ORGANIC MATTER

SEDIMENT & SOIL O_2 CONCENTRATIONS - NUTRIENT CYCLING PATHWAYS

NUTRIENT CONCENTRATIONS, SPECIATION, & ELEMENTAL RATIOS

BENTHIC PRIMARY PRODUCTION   WITHIN PLANT NUTRIENT ALLOCATION   GROWTH RATES OF RIPARIAN PLANTS

PLANT RESPONSE   PLANT
TO HERBIVORY   REPRODUCTIVE
                      STRATEGIES

STREAM PRODUCTIVITY ◄────────LITTER QUANTITY, QUALITY, & TYPE

COMPOSITION, DISTRIBUTION, AND
ARCHITECTURE OF RIPARIAN PLANT
COMMUNITY

These regions can be important source areas for soluble carbon, nitrogen, and phosphorus to the stream ecosystem and the riparian plant community. Rates of benthic primary production, within plant nutrient allocation, and the structure and growth rates of riparian plant communities are often directly linked to the concentration, speciation, and cycling rates of limiting nutrients in these environments. The interplay of geomorphology, hydrology, and biotic activity is a key variable forming and maintaining anaerobic conditions where enriched sources of nutrients are found.

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DISCLAIMER

The use of trade or product names in this chapter is for iden- tification purposes only and does not constitute endorsement by the U.S. Geological Survey.

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