



Structural dynamics of riparian forests along a black cottonwood successional gradient

Melissa K. Fierke*, J. Boone Kauffman¹

Oregon State University, Department of Fisheries and Wildlife, Nash Hall, Rm 10, Corvallis, OR, USA

Received 5 January 2005; received in revised form 25 June 2005; accepted 27 June 2005

Abstract

Black cottonwood *Populus balsamifera* L. subsp. *trichocarpa* (Brayshaw) dominated riparian forests are important habitats for organisms in both terrestrial and aquatic ecosystems in the Pacific Northwest. Using a chronosequence approach and fixed area plots, successional processes were quantified in 28 stands along 145 km of the Willamette River in Western Oregon. Cluster analysis yielded five successional stages; stand initiation, stem exclusion, early, mid, and late seral. Ordination, using non-metric multidimensional scaling, revealed stand variables were strongly associated with these groupings, e.g., stand age, cottonwood dbh, tree biomass, basal area, structural diversity. Tree densities decreased through time from a high of 96,200 to 410 trees/ha in late seral stands. Structural diversity increased through time as understory plant and late-successional tree species established in early seral stands, creating multiple vegetative layers. Aboveground standing tree biomass increased through time from <1 Mg/ha in stand initiation sites to as high as 594 Mg/ha in late seral stands. Grouping using early-successional tree species importance values revealed lower tree biomass in stands dominated by late-successional tree species when compared to late seral stands still dominated by cottonwood. Abundance of invasive plant species, e.g., reed canary grass *Phalaris arundinacea* L., appeared to negatively impact structural diversity and biomass accumulation by inhibiting understory re-initiation. A significant reduction in peak flow events in the last century may help explain the lack of riparian forest regeneration we noted, as germination and establishment of young cottonwoods was limited to low areas subject to annual flood inundation and scouring. This study reveals Willamette River black cottonwood-dominated forests as dynamic habitats consisting of a mosaic of diverse stands in varying successional stages. It is vital that we find ways to manage for regeneration of these forests as well as implementing control practices for invasive plant species.

© 2005 Elsevier B.V. All rights reserved.

Keywords: Forest succession; Riparian ecology; *Populus*; Tree biomass; Black cottonwood

1. Introduction

Black cottonwoods *Populus balsamifera* L. subsp. *trichocarpa* (Brayshaw) are majestic dominant trees along the Willamette River in West-central Oregon. They are one of the largest native hardwoods in North

* Corresponding author at: University of Arkansas, Department of Entomology, Agri. 319, Fayetteville, AR 72701, USA.
Tel.: +1 479 575 3384; fax: +1 479 575 2452.

E-mail address: mfierke@uark.edu (M.K. Fierke).

¹ Present address: Institute of Pacific Islands Forestry, Honolulu, HI 96813, USA.

America, living 150–200 years, attaining maximum sizes on nutrient-rich alluvial soils and dominating many bottomland riparian forests of the Pacific Northwest (Franklin and Dyrness, 1973; Hardin et al., 2001; DeBell, 1990). Cottonwoods are considered keystone species in many western riparian ecosystems (Johnson et al., 1976; Rood et al., 1995) and as dominant riparian tree species, play important roles in maintaining ecosystem biodiversity, both terrestrial and aquatic, through leaf litter inputs, snags, and downed wood (Sedell and Froggatt, 1984; Harmon et al., 1986; Gregory et al., 1991).

As is true with many western river systems, riparian forests along the Willamette River are only a fraction of their historical magnitude as they have been reduced to narrow discontinuous remnants due to flood control, clearing for agriculture and bank stabilization structures (Towle, 1982; Frenkel et al., 1984; Benner and Sedell, 1997; Dykaar and Wigington, 2000). These human interventions have resulted in reducing or negating natural disturbance regimes along many river systems (Johnson et al., 1976; Rood and Heinze-Milne, 1989; Rood et al., 1995). Land and water uses often result in riparian communities dominated by invasive plant species or by shade-tolerant late-successional tree species that replace senescing riparian-obligate trees (Johnson et al., 1976; Rood and Heinze-Milne, 1989; Rood et al., 1995; Barnes, 1997). As a result, riparian areas characterized by a mosaic of diverse, patchy habitats representing all successional and structural stages are declining throughout the West, becoming more homogenous with few early and mid-seral stands (Johnson et al., 1976; Rood et al., 1995; Barnes, 1997; Gutowsky, 2000). Dykaar and Wigington (2000) found few stands of young black cottonwoods along the Willamette River and suggested current rates of establishment and growth of black cottonwood were inadequate to sustain the current riparian forest area.

Despite the importance and threatened status of these riparian forests, few studies have attempted to quantify their structural characteristics and how these change through time. The objectives of this study were to quantify and describe successional change, stand development, and biomass accumulation in black cottonwood riparian forests of the Willamette River, Oregon from recently established seedlings on fresh alluvial substrate to late-successional stands.

2. Methods

2.1. Study approach

We utilized a chronosequence approach to describe succession in black cottonwood riparian forests. A chronosequence utilizes a series of stands of different ages, with the assumption that all stands were, or will be, similar in appearance when at the same age (Oliver, 1981). It is a valid approach to infer basic patterns of successional change as it is comparable to repeated measures of permanent plots (Foster and Tilman, 2000).

2.2. Study area

The study area comprised a 145-km section of the Willamette River from the cities Eugene to Salem, in Western Oregon (Fig. 1). The Willamette River is ~474 km long, drains ~31,080 km² and is the 13th largest river in terms of total discharge in the continental United States (Wentz et al., 1998). Climate is described as humid temperate with cool wet winters and warm dry summers. Average annual precipitation is 110 cm and average temperatures range from 4.4 to 26.7 °C. Agriculture dominates along most of the river with grass seed, wheat, and hay being primary crops. Several large population centers, e.g., Salem, Portland, Corvallis, Eugene, are located along the river with populations of ~2.4 million people.

2.3. Site selection

Following an initial reconnaissance, 34 stands were identified that met study criteria including the presence of black cottonwoods as a canopy layer, relatively intact with no obvious within-stand human disturbance, large enough for a plot without excessive edge effects (3 to >10 m buffer depending on stand age) and access permission granted by landowner. There was a scarcity of young stands with black cottonwood <35 cm average diameter at 1.3 m height (dbh), and all such stands identified were sampled ($n = 14$). Of the 20 older stands identified with black cottonwood >35 cm average dbh, 14 were chosen, based on spatial position along the river so as to have a relatively even dispersal along the study reach and to encompass a reasonable distribution of all size classes.

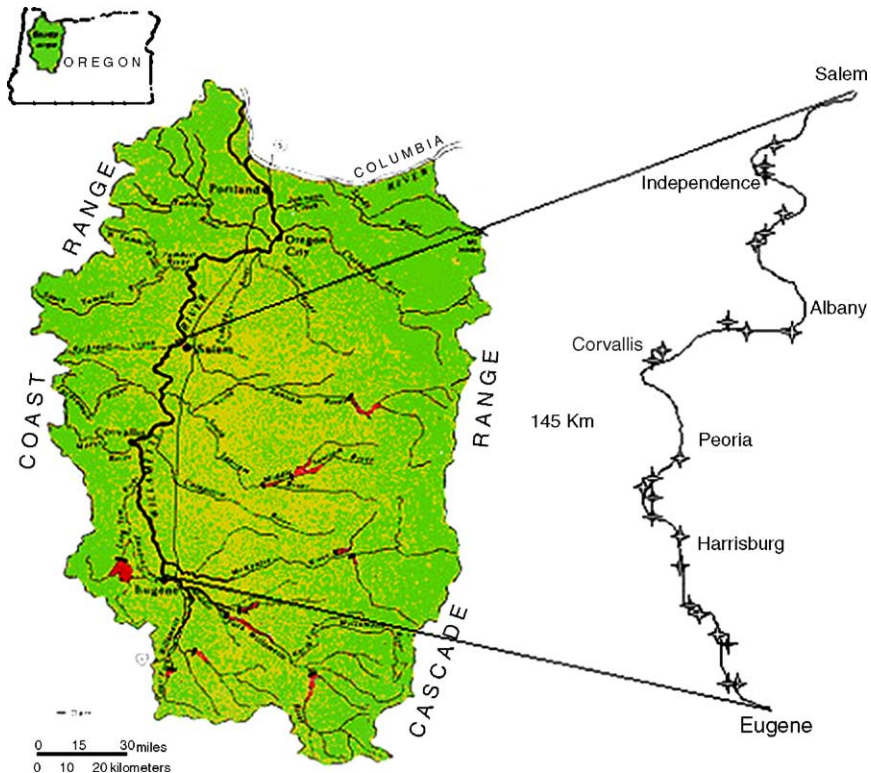


Fig. 1. Study reach along 145 km of the Willamette River from the cities of Eugene to Salem, Oregon, USA. Study stands are indicated by asterisks; note that several stands were adjacent to each other and are represented by a single symbol.

2.4. Field measurements

Five habitat variables were delineated in 28 sampled stands. Geomorphic position, riverine position, and meander position were based on fluvial processes outlined by Leopold et al. (1964) and were numbered sequentially for analysis. Geomorphic positions were gravel bar, old meander channel, and low (<3 m above the low water level), medium (3–6 m), and high (>6 m) terraces. Riverine positions included confluence, single channel form and multiple channel form. Meander positions were inside a meander curve, outside a meander curve, or along a straight section of the river. Longitudinal position or river km was determined from Willamette river maps (Smith et al., 1995) and 1996 aerial photos. Stand area was calculated from 1996 digitized aerial photos.

Structural characteristics and biomass along a successional gradient were quantified using a nested plot design. Macroplots (30 m × 100 m; 0.30 ha)

were arbitrarily established and were considered the sample unit. Species and dbh were determined for trees and standing dead trees >10 cm dbh (hereafter referred to as large trees). Vascular plant nomenclature follows Gilkey and Dennis (2001) and Hitchcock and Cronquist (1973). Height was measured for all snags using a clinometer. Height was determined for two to five live cottonwoods chosen to represent a variety of size-classes in order to derive a regression equation for height and dbh. These trees were also cored at breast height using an increment borer for age determination.

Trees >1.3 m in height and <10 cm dbh (hereafter referred to as small trees) and volume of downed wood were measured in 4 m × 50 m subplots nested along the leading edge and the centerline of the macroplot. In nine early-successional stands (average dbh <15 cm), trees and snags were measured within 4 m × 50 m plots; this was a necessary modification as all stands of these size classes were <3000 m². In dense (>350 stems/50 m²) stem exclusion stands,

trees were measured in a 2 m × 25 m subplot nested along the centerline of the 4 m × 50 m plot.

Cover was estimated to the nearest whole percent for each understory species in twenty 50 cm × 50 cm nested microplots placed randomly within the 30 m × 100 m or the 4 m × 50 m sample plot. Tree seedling (<1.3 m height) density and vertical structural diversity were also estimated within microplots. For vertical structural diversity, presence or absence of six synusia, or vegetative layers, within the 50 cm × 50 cm microplots was determined as projected vertically from ground level through the canopy layer. These layers were herbaceous, low shrub (<0.5 m in height), tall shrub (>0.5 m in height), low tree (<5 m in height), mid-tree (>5 m, but not cottonwood), and canopy (cottonwood). Tall shrubs and low trees were differentiated by species. Microplot values were averaged to represent sample plot mean.

2.5. Stand age

Approximate stand age was determined using a combination of dendrochronology and aerial photo interpretation. Cores were extracted from at least two, and up to six trees in stands with cottonwoods <50 cm dbh ($n = 20$). Cores were dried and rings counted under a dissecting microscope. Sites with trees >50 cm dbh were generally not cored. Young stands were relatively easy to age; however, those from older stands were progressively harder to age precisely as cores removed from older trees at several sites exhibited indistinct rings and extensive spongy areas, rendering rings virtually indistinguishable. A large increment borer was unavailable early in the study but due to our inability to distinguish rings in older trees, purchase of large borer was not justified. A review of aerial photos was conducted to confirm stand ages from tree cores and provide a window of establishment. Willamette River aerial photos were available for 15 different years ranging from 1936 to 1996. Six sampled stands established prior to 1936 and so were labeled as >65 years old.

2.6. Biomass equations

Allometric diameter–height relationships were determined for black cottonwood using standard

regression techniques of measurements for height and diameter of 61 trees from 20 stands (Table 1). Live tree biomass was determined using published biomass equations except for black cottonwoods >30 and <5 cm dbh (Table 1).

Biomass equations for black cottonwoods >30 cm dbh were developed using published bole volume equations, black cottonwood wood density and calculated component biomass relationships. Inside-bark bole volume was determined using a British Columbia volume equation for black cottonwoods (British Columbia Forest Service, 1983) and the above derived height equation. Bole volume was then multiplied by average black cottonwood wood density, or specific gravity (0.33 dry g/fresh cm³) (United States Forest Products Laboratory, 1974) to get bole biomass. Biomass of other components, foliage, branches and bark, was calculated to be 67% of bole biomass using mean biomass component relationships from Standish et al. (1985) biomass equations.

For 0–5 cm dbh black cottonwoods, allometric dbh–biomass relationships were determined using standard regression techniques. Five trees with dbh ranging from 0.1 to 3.9 cm were selected from 4 early seral sites ($n = 20$) to represent a continuum of sizes within each stand. Trees were harvested, returned to the lab, oven-dried to a constant mass, and weighed.

Snag biomass was determined by first calculating volume (m³) using a frustum of a cone equation:

$$V = \pi \left(\frac{H}{3} \right) (r_1^2 + r_1 r_2 + r_2^2)$$

where H is bole height, r_1 is radius at base and r_2 is radius of top. A taper equation was derived, based on downed wood measured in this study, to estimate r_2 for snags:

$$r_2 = r_1 - CD$$

where change in diameter, $CD = 1.074H + 0.8418$ (d.f. = 206; $R^2 = 0.683$; $P < 0.0001$). Biomass was calculated by multiplying volume by average downed wood density ($0.327 \pm \text{S.E. } 0.019$ dry g/fresh cm³). Downed wood specific gravity was determined by immersion measurement (Krahmer and Van Vliet, 1983) of 40 wood samples collected randomly from 10 field sites. This value was also used for snags.

Table 1

Equations used to determine aboveground tree biomass (Mg) in black cottonwood-dominated riparian forests

| Parameter | Equation | <i>n</i> | <i>R</i> ² |
|--|--|----------|-----------------------|
| H: <i>Populus balsamifera</i> ^a | $-0.005 \times D^2 + 1.014 \times D + 3.289$ | 61 | 0.93 |
| BV: <i>Populus balsamifera</i> >30 cm dbh ^b | $10^{-4.648+1.735 \times \log D + 1.356 \times \log H}$ | 347 | * |
| TB: <i>Populus balsamifera</i> >30 cm dbh ^a | $((BV \times SG) \times 0.67) + (BV \times SG)$ | – | – |
| TB: <i>Populus balsamifera</i> 5–30 cm dbh ^c <i>Salix</i> spp. ^{**c} | $(7.4 + 156.4 \times D^2 \times H)/10^3$ | 30 | 0.95 |
| TB: <i>Populus balsamifera</i> <5 cm dbh ^a <i>Salix</i> spp. ^{**a} | $(160.06 \times D^2 + 8.48 \times D)/10^6$ | 20 | 0.97 |
| TB: <i>Fraxinus latifolia</i> ^{**d} , <i>Crataegus douglasii</i> ^{**d} , <i>Rhamnus purshiana</i> ^{**d} | $(0.1063 \times D^{2.480})/10^3$ | 18 | N/A |
| TB: <i>Acer macrophyllum</i> ^e | $(e^{-3.765+1.617 \times \ln D} + e^{-4.236+2.430 \times \ln D} + e^{-2.116+1.092 \times \ln D} + e^{-3.493+2.723 \times \ln D} + e^{-4.574+2.574 \times \ln D})/10^3$ | 18 | 0.15–0.99 |
| TB: <i>Quercus garryana</i> ^{**f} | $(0.0293 \times D^{2.866})/10^3$ | 22 | 0.94 |
| TB: <i>Prunus</i> spp. ^{**g} | $(0.0716 \times D^{2.617})/10^3$ | 26 | 0.99 |
| TB: <i>Cornus sericea</i> ^{**h} | $(e^{3.294+2.063 \times \ln D_b} + e^{2.261+2.874 \times \ln D_b} + e^{2.792+1.869 \times \ln D_b})/10^6$ | 18 | 0.78, 0.84 |
| TB: <i>Corylus cornuta</i> var. <i>californica</i> ^h , <i>Oemleria cerasiformis</i> ^{**h} , <i>Sambucus racemosa</i> ^{**h} | $(e^{2.417+2.040 \times \ln D_b} + e^{3.719+2.989 \times \ln D_b})/10^6$ | 18 | 0.82, 0.89 |

Abbreviations: TB, tree biomass (Mg); *H*, height (m); BV, bole volume (m³); *D*, diameter at breast height (cm); *D*_b, diameter at base (cm); SG, specific gravity (dry g/fresh cm³). Sources are indicated by superscript numbers following parameter description.

^a This study (see text for details).

^b British Columbia Forest Service (1983).

^c Standish et al. (1985).

^d Perala and Alban (1994).

^e Grier and Logan (1978).

^f Bridge (1979).

^g Breneman et al. (1997).

^h Gholz et al., 1979.

* Standard error was 10.6, *R*² not provided.

** Indicates species substitutions.

Total aboveground tree biomass (TATB) consisted of snag biomass and both small and large living tree biomass. Average annual biomass accumulation (ABA) for each sampled site was calculated by dividing TATB by stand age. For stands >65 years old, 65 was used to estimate ABA. This resulted in values for late successional stands that were likely overestimated, however, if these ABA values prove to be significantly lower than for earlier successional stages, the trend for decreased ABA would be valid and the information considered valuable.

Shrubs, herbs, grasses/sedges and forest floor litter biomass were not included in estimates of TATB. These components were <0.5% of aboveground live tree biomass as documented by a pilot study involving four study sites where understory vegetation and litter biomass components were measured in 11–50 cm × 50 cm microplots, and ranged from 0.93 to 1.48 Mg/ha. This number is comparable to another understory biomass study of *Populus* sp. stands (0.9–1.7 Mg/ha, Bray and Dudkiewicz, 1963).

2.7. Forest structure equations

The Shannon diversity formula (Shannon, 1948) was used to calculate vertical structural diversity (*H'*) as it considers both number of layers present and evenness of the presence of layers. Antilog of *H'* was calculated, making the estimated diversity value comparable to the original maximum measurement, e.g., 10^{*H'*} = 6.0 indicates that all 6 vegetative layers were present in all microplots.

Relative dominance of tree species within each sampled stand was determined by calculating importance values (Johnson et al., 1976). Importance value was based on relative frequency and relative basal area of trees >10 cm dbh within a macroplot,

$$IV = \frac{F_s/F_t + B_s/B_t}{2 \times 100}$$

where *F*_s is frequency of a particular tree species, *F*_t is total number of all trees, *B*_s is basal area of a tree species, and *B*_t is total tree basal area. Importance

value of pioneer tree species was calculated by combining data for black cottonwood and willow species in each plot.

2.8. Analysis

All understory species were placed into one of four categories and cover estimates for these categories yielded the following variables, tall shrub cover, low shrub/vine cover, herbaceous cover, and grass/sedge cover. These were included with other stand variables measured and calculated, e.g., mean cottonwood dbh, mean TATB, etc., to yield a data matrix of 28 sites \times 20 variables. These data were analyzed using cluster analysis and non-metric multidimensional scaling (NMS) in PCORD (MjM Software, Gleneden Beach, Oregon) following methods of McCune and Grace (2002). The purpose of cluster analysis was to group sampled stands by variables to yield groupings related to discrete successional stages. The purpose of NMS ordination was to provide a graphical depiction of stand relationships and determine variables strongly correlated with successional groupings.

Data were transformed using the general relativization option to make variables equally important relative to each other. Outlier stands were identified by examining a frequency distribution of average Sorensen distance between each sample unit and other sample units in space. Two sample units were identified as outliers, however, they were retained as they were only weak outliers with average distances of <2.5 standard deviations larger than the mean. Cluster analysis was performed using Sorensen distance measure and Ward's group-linkage method. Ordination was performed using NMS autopilot mode with the slow and thorough option with Sorensen distance measure and the best of 40 runs with real data along with 50 runs with randomized data for a Monte Carlo test of significance. Sites close together in habitat space were most similar. The matrix of stand and habitat variables was overlain on the resulting ordination using a joint plot. Overlays were based on correlations of variables with axes of the ordination. Relative importance of relationships to each axis is indicated by the length and direction of lines that represent individual variables. Ordinations were rigidly rotated to load the strongest variable onto Axis 1,

maximizing proportion of variance explained by that axis or variable (McCune and Grace, 2002).

Statistical analyses were done in JMP 5.1 (SAS Institute, 2004). Analysis of variance and Tukey–Kramer HSD means comparison test were used to determine significant differences in variables between successional stages, in TATB between groupings based on pioneer tree species importance values and in small tree abundance and vertical structural diversity between cover classes of reed canarygrass *Phalaris arundinacea* L. The first analysis was done in order to establish quantifiable differences in individual stand and habitat variables between successional stages derived from cluster analysis. The second analysis was to demonstrate differences in TATB between stands dominated by cottonwood versus what might be expected in late seral stands dominated by shade-tolerant late-successional tree species. The last was to ascertain if statistical analysis could confirm field observations of fewer small trees and decreased vertical structural diversity in stands with high percent cover of reed canarygrass.

Analysis of variance and regression analysis were used to test for significant relationships between variables of interest, Table 2. Analysis of stand data was to discern trends as related to stand age and successional processes occurring over time. Peak stream flow events were examined for the Willamette River gaging station at Albany, Oregon (USGS, 2001) from 1862 to 2001 in an effort to discern why we found few stem exclusion and early seral stands. Regression models employed were linear, logarithmic, polynomial, power, and exponential. Results given were for the model resulting in maximum variation explained as represented by the largest coefficient of determination (R^2).

3. Results

3.1. Succession

Measurements of 2201 large trees, 1763 small trees, and 137 seedlings in 560 microplots yielded stand and structural data for the sampled 28 stands. Cluster analysis yielded five groups when cut at 70% information retained (Fig. 2). This cut was chosen as the length of lines indicated differences in groups

Table 2
Variables used in regression analysis

| Independent variable | Dependent variable | Description |
|----------------------|-------------------------------|--|
| Stand age | Aboveground tree biomass | Large tree, small tree and snag biomass (Mg/ha) |
| | Pioneer tree species IV | Importance value of cottonwood and willow spp. |
| | Cottonwood dbh | Mean cottonwood dbh (cm) |
| | Basal area | Basal area of live trees (m ² /ha) |
| | Vertical structural diversity | H' based on presence of 6 vegetative layers |
| Year | Peak streamflow events | Peak events from 139 years of record (m ³ /s) |

while retaining the greatest amount of information. These groups were designated as: stand initiation, stem exclusion, early, mid, and late seral.

Non-metric multi-dimensional scaling of sites based on stand and habitat data resulted in a two-dimensional ordination (Fig. 3). Stress (8.1) was statistically significantly reduced compared to randomized data in the Monte Carlo test and the final ordination was stable. After rigid rotation of 159° to load the strongest variable onto Axis 1, 96.2% of variation was explained, 86.4% by Axis 1 and 9.8% by Axis 2.

An overlay of the 20 stand and habitat variables revealed that all variables were significantly correlated ($r > 0.20$) with one of the axes and sometimes, both.

Vertical structural diversity, stand age, cottonwood dbh, large tree biomass, and basal area were most strongly positively correlated with Axis 1 ($r = 0.92$ – 0.87). Six other variables were also significantly positively correlated ($r = 0.79$ – 0.53) with Axis 1 and seven variables were negatively associated ($r = -0.76$ to -0.22). Four variables were significantly positively correlated with Axis 2 ($r = 0.67$ – 0.27) and six variables were negatively associated ($r = -0.66$ to -0.24).

Grouping stands based on percent cover of reed canary grass derived from microplot cover measurements revealed that total numbers of small trees were significantly lower in stands with >15% reed canary grass cover, mean 1554 (SE 261) versus 250

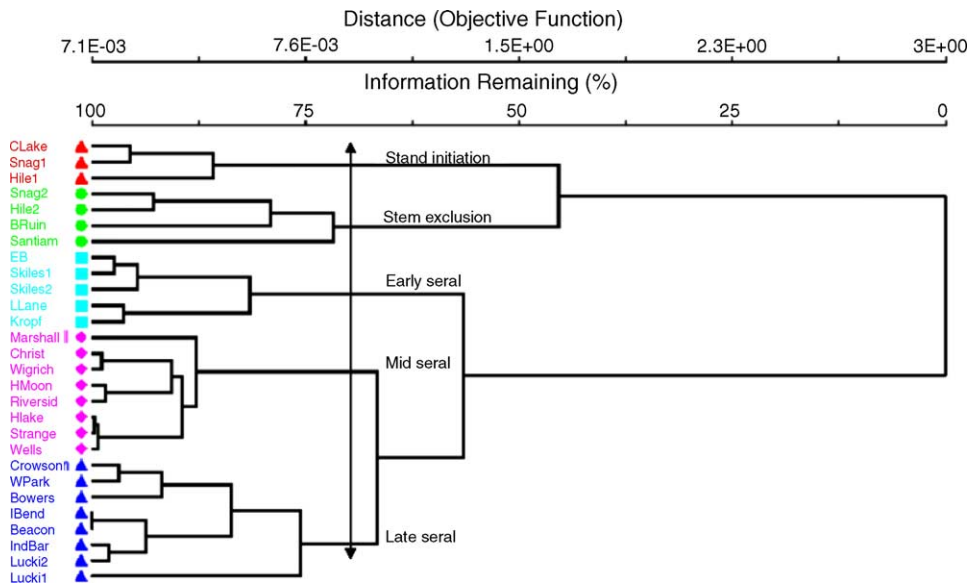


Fig. 2. Results of cluster analysis of 28 Willamette River riparian forests and assignment of stands to successional stages using 20 stand and habitat variables. Groups were cut at 70% information remaining to maximize information retained while selecting definitive groups based on length of lines leading into groups.

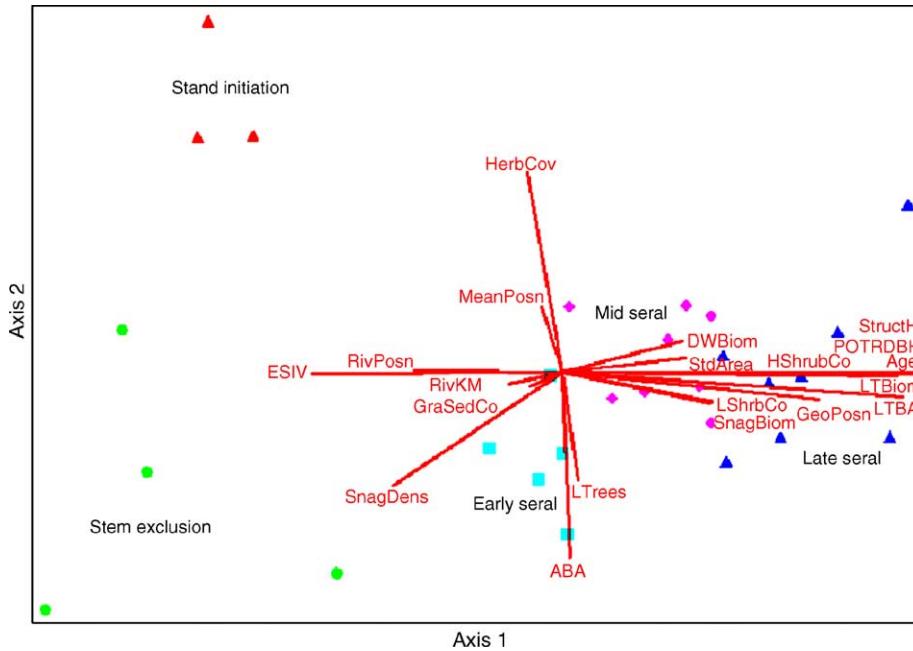


Fig. 3. Results of NMS ordination of 28 sampled stands with a joint plot overlay of 20 stand and habitat variables. Length and direction of lines indicate relationship of variables with each axis. Abbreviation definitions: ESIV, early-successional tree species importance values; RivPosn, river position; MeanPosn, meander position; HerbCov, herbaceous cover; DWBiom, downed wood biomass; StdArea, stand area; HShrubCo, tall shrub cover; StructH, vertical structural diversity; POTRDBH, cottonwood dbh; Age, stand age; LTBIom, large tree biomass; LTBA, large tree basal area; GeoPosn, geomorphic position; LShrubCo, low shrub cover; SnagBiom, snag biomass; LTrees, large tree density; ABA, annual biomass accumulation; SnagDens, snag density; GraSedCov, grass/sedge cover, RivKM, river kilometer.

(91) trees/ha (d.f. = 1, 15; $P = 0.0195$, Fig. 4). When small trees were separated into groups based on late-successional versus understory tree species, there significantly fewer understory trees at 1081 (232)

versus 110 (58) trees/ha (d.f. = 1, 15; $P = 0.0331$) in stands with high reed canarygrass cover, but not significantly different numbers of late-successional trees 256 (61) versus 90 (40) trees/ha (d.f. = 1, 15;

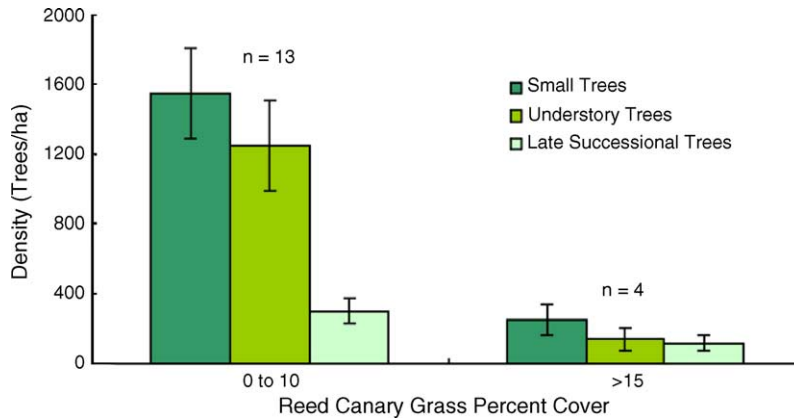


Fig. 4. Reed canary grass abundance vs. small tree densities (<10 cm dbh) in stands >15 years old. Bars represent standard error. Small trees include both understory and late-successional trees; species were placed into understory or late successional categories based on descriptions from nomenclature references.

Table 3

Mean stand data based on developmental stage for 28 riparian stands along the Willamette River, Oregon

| Stand variable | Stand initiation (3) | Stem exclusion (4) | Early seral (5) | Mid seral (8) | Late seral (8) |
|---------------------------------|---------------------------------|-------------------------------|---------------------------|--------------------------|--------------------------|
| Stand age | 2.3(0.3) 2–3 A | 5.3 (0.6) 4–7 A | 13.4 (0.9) 12–16 A | 39 (5.6) 22 to >65 B | >65 45 to >65 C |
| Large tree density (trees/ha) | – | 288 (288) 0–11501 B | 982 (133) 633–1350 A | 415 (34) 303–583 B | 271 (23) 183–390 B |
| Small tree density (trees/ha) | 8500 (4278) 0–136000 A | 49212 (21912) 4050–96200 B | 810 (310) 150–1950 A | 1238 (376) 100–2800 A | 1475 (355) 150–3450 A |
| Seedling density (seedlings/ha) | 54000 (27592) 12000–106000 A | 5000 (2887) 0–10000 B | 800 (800) 0–4000 B | 7750 (4096) 0–32000 B | 3250 (1601) 0–12000 B |
| Vertical structural diversity | 2.7 (0.5) 2–3.6 A | 2.3 (0.1) 2.2–2.4 A | 4.8 (0.3) 3.9–5.8 B | 5.4 (1.9) 4.1–5.7 B | 5.6 (0.1) 5.1–5.8 B |
| Cottonwood dbh (cm) | 0.57 (0.2) 0.3–0.8 A | 3.7 (2.1) 4–9.9 A | 18 (2.2) 11–23 A | 48 (4.3) 29–62 B | 62.5 (4.3) 49–89 B |
| Basal area (m ² /ha) | 0.3 (0.3) <1–4 A | 19.5 (6.6) 4–34 AB | 34 (3.3) 24–44 BC | 37 (2.1) 30–46 BC | 47 (3.8) 29–62 C |
| Snag biomass (Mg/ha) | 0 (0) 0 A | 0.73 (0.7) 0–2.2 A | 1.3 (0.8) 0–4.1 A | 1.7 (0.5) 0–3.5 A | 7.5 (1.6) 1.8–12.7 B |
| TATB (Mg/ha) | 0.6 (0.32) <0.1–1.1 A | 56 (28) 8.7–136 AB | 186 (24) 131–272 BC | 302 (25) 214–409 C | 437 (38) 260–594 D |
| ABA (Mg/ha/year) | 0.3 (0.1) <0.1–0.4 A | 9.6 (3.7) 1.7–19.4 BC | 14.1 (2.2) 10.9–22.6 C | 8.5 (0.9) 4.8–11.4 BC | 7.1 (0.6) 4.0–9.1 AB |

Number of stands in each stage is given in parentheses after stage, standard error is given in parentheses after means and stand mean ranges are given below means. Different letters within rows indicate significant differences using Tukey HSD means comparison at $\alpha = 0.05$.

$P = 0.16$). Vertical structural diversity was also negatively impacted (d.f. = 1, 15; $P = 0.015$) as stands with high reed canarygrass cover had significantly lower structural diversity at 5.05 than stands with low cover at 5.6.

3.2. Forest structure

There were significant differences in variables between stand stages derived from cluster analysis (Table 3). Stand initiation and stem exclusion sites were less than 7 years old and dominated by pioneer tree species, black cottonwood and willow. Cottonwood seedling and small tree densities in these sites were high compared to other stages. Early seral stands were between 10 and 20 years old and had large numbers of large trees. Understory and late-successional small tree and seedling densities were variable in stands >10 years old ($n = 21$). Few synusia were present during stand initiation and stem exclusion stages but with the onset of understory re-initiation,

vertical structural diversity increased from early to late seral stages.

Trees were larger in mid and late seral stands as evidenced by increasing black cottonwood dbh (maximum of 128.5 cm dbh) and tree basal area. Snag biomass was low in stand initiation and stem exclusion stands, but increased in later successional stages. In stand initiation, stem exclusion, and early seral stands, black cottonwood biomass accounted for 81–100% of TATB compared to 52–96% in mid and late seral stands. Small tree biomass (not given in table) generally accounted for <3% of TATB in mid to late seral stands and ranged from <1 to 7 Mg/ha.

Annual biomass accumulation (ABA) was significantly different between stages and reached a maximum in early seral stands. Trends through time were that ABA increased sharply from stand initiation into stem exclusion and early seral sites and then decreased in later stages. Values for late seral sites could be somewhat less as stands older than 65 years

would have lower values than those calculated, but the decreasing ABA trend from early seral stands is valid.

Regression analysis revealed that pioneer tree species importance values were negatively correlated with stand age and best described using a polynomial equation (Fig. 5A). Cottonwood dbh, tree basal area, and TATB were positively correlated with stand age and were best described with a polynomial and with logarithmic equations, respectively (Fig. 5B–D).

Vertical structural diversity increased linearly for ~15 years but is best described by a polynomial line in stands past stem exclusion (Fig. 5E).

When grouped based on pioneer tree species importance values (IV), TATB peaked at a maximum mean of 464 Mg/ha in late seral stands where black cottonwood remained the dominant tree species, mean IV = 55 (Fig. 6). Groups with average pioneer IV of >77 had significantly lower average biomass as did

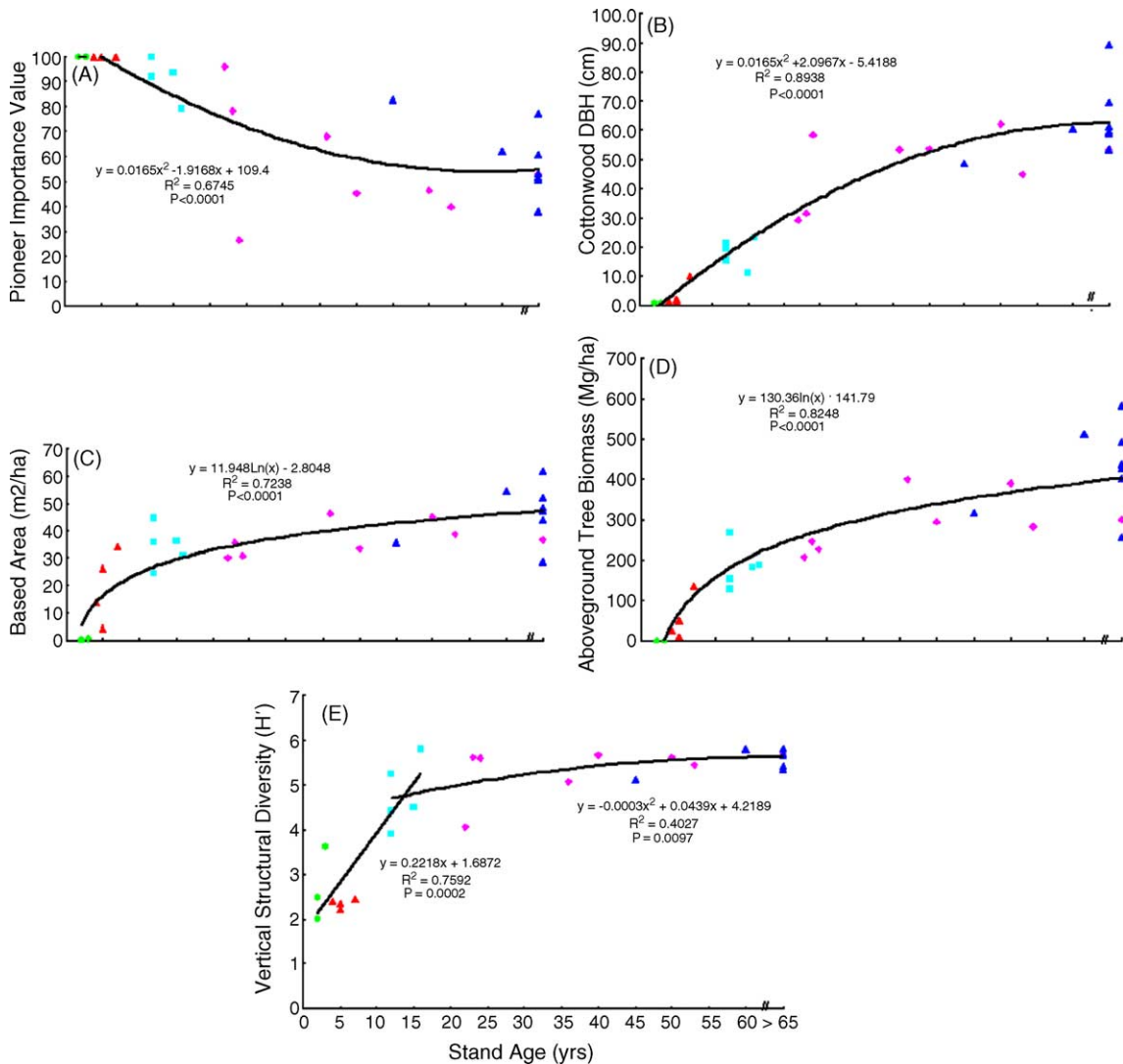


Fig. 5. Regression analysis reveals significant changes in forest structural characteristics of Willamette River riparian forests through time. Note differences in y-axis labels.

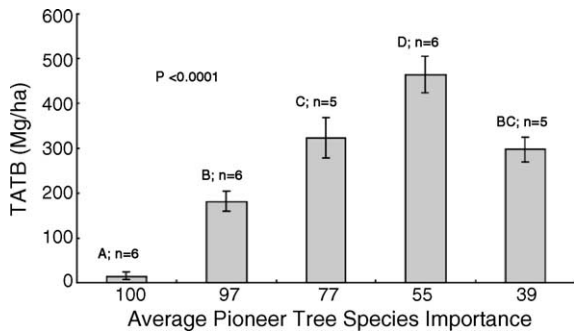


Fig. 6. Total aboveground tree biomass based on importance value of early-successional tree species in Willamette River riparian forests. Bars are standard errors. Groups with different letters are significantly different (Tukey–Kramer HSD, $\alpha = 0.05$). Importance values were determined using relative frequency and relative basal area of pioneer tree species.

stands dominated by late-successional tree species with a mean of 297 Mg/ha.

3.3. Stand establishment

Linear regression analysis of peak flow events indicated a significant decrease (d.f. = 116; $P < 0.0001$) in the magnitude of flood events in the past 139 years (Fig. 7).

4. Discussion

4.1. Succession

Groups derived in this study can be compared to hypothesized major disturbance-initiated successional stages of stand initiation, stem exclusion, understory re-initiation, and old growth as described by Oliver

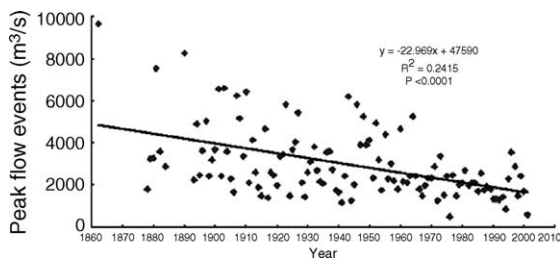


Fig. 7. Linear regression analysis of peak flow events recorded at the Willamette River Albany gaging station from 1860 to 2001.

(1981). However, succession in these black cottonwood-dominated floodplain forests is different as there are no late-successional tree species present in stand initiation and stem exclusion stands. Late-successional trees do not establish in these forests until the understory re-initiation phase and so to more accurately describe these riparian forest successional stages, we used early, mid, and late seral to describe forests after stem exclusion.

Stand initiation of Willamette River black cottonwood-dominated riparian forests begins with seedling establishment on recently deposited moist alluvial substrate. Dominant pioneer tree species were black cottonwood and willow. These sites always occurred on gravel bars in geomorphic positions subject to scouring and excessive inundation during high winter flow events. Stand development proceeded through a “stem exclusion” phase from ~5 to 10 years post-establishment. This phase was characterized by large numbers of small pioneer trees and snags as weaker individuals died. Early seral stands were characterized by understory re-initiation, when shade-tolerant late-successional tree species, understory trees, shrubs, and herbs germinate and establish. Some common understory tree species were Indian plum *Oemlaria cerasiformis* (Hook. and Arn.) Landon and beaked hazel *Corylus cornuta* Marsh. subsp. *californica* (D.C.) E. Murray. Late-successional tree species included Oregon ash *Fraxinus latifolia* Benth. and big-leaf maple *Acer macrophyllum* Pursh. Late-successional trees were defined as those species that are able to germinate and establish in shade and at some point later in the successional process will become dominant overstory tree species. Mid and late seral stages were characterized by large black cottonwoods and increasing densities of late-successional tree species.

A few early, mid, and late seral stands did not exhibit understory re-initiation. Field observations of reed canary grass in young stands indicated that it might have been responsible for inhibiting understory and late-successional tree species establishment. Reed canary grass is an invasive grass species that forms a dense mat and can prohibit germination and establishment of native plant species (Apfelbaum and Sams, 1987). Analysis of stands >15 years old, which were grouped based on cover of reed canarygrass, indicated that there were significantly fewer small trees in stands

with >15% reed canary grass cover and that these stands had significantly lower structural diversity. Variability in small tree numbers did occur in some stands with <15% reed canary grass cover. Alternative explanations for these stands may have been high black cottonwood density, high density of native herbs and grasses, or high densities of other invasive non-native plant species, e.g., Himalayan blackberry *Rubus armeniacus* L., English ivy *Hedera helix* L. In the four stands with >15% cover, however, there was minimal variability with all stands having few small trees present.

4.2. Forest structure

Stand initiation and stem exclusion stands were dominated by small early-successional tree species while late seral stands had large old cottonwoods and some were dominated by late-successional tree species. Density of standing dead trees peaked during stem exclusion as fitter individuals out-competed others for available resources, e.g., water, nutrients, light. Large tree (>10 cm dbh) densities from 183 to 1350 trees/ha and basal areas of 28–61 m²/ha found in this study were somewhat greater than those found in Missouri River cottonwood riparian forests. Johnson et al. (1976) found density of trees >10.2 cm dbh ranged from 93 to 1105 trees/ha and basal area from 16 to 57 m²/ha in North Dakota plains cottonwood *Populus deltoides* Bartr. ex Marsh. riparian stands.

Few synusia were present during stand initiation and stem exclusion stages, but as stands opened up during early seral stages and understory re-initiation commenced with the germination and establishment of understory and late-successional tree species, herbs, grasses, and shrubs, multiple vegetative layers developed and structural diversity increased. Pioneer tree species are shade intolerant and unable to germinate and establish beneath their own canopy and so decrease in importance as stands age. Shade-tolerant late-successional tree species are able to establish and increase in biomass and density under cottonwood canopy, provided an intervening disturbance does not occur, and thus increase in dominance over time. There was a broad range of ages at which this occurred from 24 to >65 years. Late in succession, though, as cottonwoods senesce and drop out as the canopy layer, there is a decrease in the

maximum number of vegetative layers possible and structural diversity will likely decrease.

These black cottonwood forests are large in stature and biomass compared to other riparian forest communities. Maximum biomass of late seral forests in this study were more than twice that of Montana cottonwood riparian forests and Northeastern Oregon conifer-dominated riparian forests. Boggs and Weaver (1994) reported biomass of plains cottonwood forests ranged from 147 to 193 Mg/ha along the lower Yellowstone River and Mcase (1995) found that biomass ranged from 203 to 261 Mg/ha in coniferous riparian forests along the Grande Rhonde River. In fact, the maximum TATB value of 594 Mg/ha in one late seral stand rival those calculated by Grier and Logan (1977) for old growth coniferous riparian forest stands in the Cascade Mountains of Oregon (589–667 Mg/ha).

Total aboveground tree biomass reached a maximum in late seral forests where black cottonwoods were still dominant. In late seral stands where shade-tolerant late-successional tree species, Oregon ash and big-leaf maple, were dominant, tree biomass was lower. These late-successional tree species do not have the potential at maturity to achieve the physical dimensions possible for black cottonwood (Owston, 1990; Minore and Zasada, 1990; DeBell, 1990) and so it is likely that maximum biomass is achieved when black cottonwood is still dominant.

These forests demonstrate high rates of growth and biomass accumulation compared to many forests of the world. Annual biomass accumulation rates between 11 and 23 Mg/ha/year were highest in early seral forests, which were higher than rates found in Mexican tropical secondary forests (3–19 Mg/ha/year; Hughes et al., 1999). Accumulation rates were lower in late seral stands as black cottonwood senesce and late-successional tree species come to dominate, and even though these late-successional species were young and growing their ABA rates evidently are not comparable to young black cottonwood ABA rates. Late seral ABA rates, 4–9 Mg/ha/year, were, however, higher than the 1.8–2.6 Mg/ha/year found in old growth Cascade coniferous riparian forests by Grier and Logan (1977). Again, though late seral ABA values were based on 65 years and so may be lower than indicated, but even at half of the estimated values they would still be higher.

4.3. Stand establishment

Initial recognizance revealed few young stands in geomorphic positions favorable to long-term stand establishment. Based on this, peak flow events over 141 years were examined for the Albany gaging station on the Willamette River. In 1862, the largest flood event on record occurred at 9628 m³/s. Since that time, there have been no floods greater than 8300 m³/s and only 9 floods >5500 m³/s, all of which occurred prior to 1947. Gregory et al. (2002) noted that 11 flood control reservoirs constructed by the Army Corps of Engineers between 1949 and 1964 have dampened peak flows by 30–50%. Reduced flood events have also been associated with declines in riparian forests in other river systems (Rood and Heinze-Milne, 1989) and so may very well be a major contributor to reduced regeneration on the Willamette River.

5. Conclusions

Riparian forests play multiple functional roles affecting water quality as well as aquatic and terrestrial biodiversity. There are numerous threats to these forests, e.g., urbanization, agriculture, invasive species, flow management, etc. In this study, we provide a quantitative description of succession and forest structure along a successional gradient in Willamette River black cottonwood riparian forests. Despite not knowing exactly how many young stands are necessary to maintain riparian forest regeneration along this river system, we strongly suggest, as did Dykaar and Wigington (2000), that stands along this riverine system are not regenerating in a manner to sustain the current aerial extent of forests. We also provide evidence that decreases in peak flow events are likely responsible for reduced turnover and renewal of these floodplain forests. Our results indicate that structural diversity and biomass will decline as the current forests become dominated by late-successional species. There will be impacts on both terrestrial and adjacent aquatic systems as black cottonwoods decline in importance, changing downed wood and allochthonous inputs into both systems. Over time, if no effort is made to ensure a mosaic of riparian forests of differing age and compositional structure in this river system, structural and biological

diversity will decrease in Willamette River riparian forests.

Acknowledgements

We thank Brad Fierke, Mindy Simmons, and Joe Means for field and intellectual assistance and unidentified reviewers for edits to the original manuscript. This research was made possible through a NSF GK-12 Fellowship.

References

- Apfelbaum, S.I., Sams, C.E., 1987. Ecology and control of reed canarygrass. *Nat. Areas J.* 7, 69–74.
- Barnes, W.J., 1997. Vegetation dynamics on the floodplain of the lower Chippewa River in Wisconsin. *J. Torr. Bot. Soc.* 124, 189–197.
- Benner, P.A., Sedell, J.R., 1997. Upper Willamette River landscape: a historic perspective. In: Laenen, A., Dunnette, D.A. (Eds.), *River Quality: Dynamics and Restoration*. Lewis Publishers, New York, pp. 23–47.
- Boggs, K., Weaver, T., 1994. Changes in vegetation and nutrient pools during riparian succession. *Wetlands* 14, 98–109.
- Bray, J.R., Dudkiewicz, L.A., 1963. The composition, biomass and productivity of two *Populus* forests. *Bull. Torr. Bot. Club.* 90, 298–308.
- Brenneman, B.B., Frederick, D.J., Gardner, W.E., Schoenhofen, L.H., Marsh, P.L., 1997. Biomass of species and stands of West Virginia hardwoods. In: Pope, P.E. (Ed.), *Proceedings of Central Hardwood Forest Conference II*. Purdue University, West Lafayette, Indiana, pp. 159–178 (As presented in: Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. *For. Ecol. Manage.* 97, 1–24).
- Bridge, J.A., 1979. Fuelwood production of mixed hardwoods on mesic sites in Rhode Island. M.S. Thesis. University of RI, Kingston, RI. p. 72 (As presented in: Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. *For. Ecol. Manage.* 97, 1–24).
- British Columbia Forest Service, 1983. Whole stem cubic metre volume equations and tables centimetre diameter class merchantable volume factors, 1976. In: Watts, S.B. (Ed.), *Forestry Handbook for British Columbia*. fourth ed. Forestry Undergraduate Society, Vancouver.
- Case, R.L., 1995. The ecology of riparian ecosystems of Northeast Oregon: shrub recovery at Meadow Creek and structure and biomass of headwater Upper Grande Ronde ecosystems. M. Sc. thesis. Department of Fisheries Science, Oregon State University, Corvallis, Oregon.
- DeBell, D.S., 1990. *Populus trichocarpa* Torr. and Gray: black cottonwood. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North American Hardwoods*, vol. 12, USDA Handbook. pp. 570–576.

- Dykaar, B.B., Wigington Jr., P.J., 2000. Floodplain formation and cottonwood colonization patterns on the Willamette River, Oregon, USA. *Environ. Manage.* 25, 87–104.
- Foster, B.L., Tilman, D., 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. *Plant Ecol.* 146, 1–10.
- Franklin, J.F., Dyrness, C.T., 1973. *Natural Vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, Oregon.
- Frenkel, R.E., Wickramaratne, S.N., Heinitz, E.F., 1984. Vegetation and land cover change in the Willamette River greenway in Benton and Linn counties, Oregon: 1972–1981. *Assoc. Pac. Coast Geogr. Ybk.* 46, 64–77.
- Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T., 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Lab, Oregon State University, Corvallis, Oregon.
- Gilkey, H.M., Dennis, L.R.J., 2001. *Handbook of Northwestern Plants*. Oregon State University Press, Corvallis, OR.
- Gregory, S.V., Swanson, F.J., McKee, W.A., Cummins, K.W., 1991. An ecosystem perspective of riparian zones. *Bioscience* 41, 540–551.
- Gregory, S.V., Ashkenas, L., Jett, S., Wildman, R., 2002. Flood inundations/FEMA floodplains. In: Hulse, D., Gregory, S.V., Baker, J. (Eds.), *Willamette River Basin Planning Atlas: Trajectories of Environmental and Ecological Change*. Oregon State University Press, Corvallis, OR.
- Grier, C.C., Logan, R.S., 1978. Old-growth Douglas-fir communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* 47, 373–400.
- Gutowsky, S.L., 2000. Riparian cover changes associated with flow regulation and bank stabilization along the Upper Willamette River in Oregon between 1939 and 1996. M. Sc. thesis. Department of Geosciences. Oregon State University, Corvallis, Oregon.
- Hardin, J.W., Leopold, D.J., White, F.M., 2001. *Harlow and Harrar's Textbook of Dendrology*. McGraw-Hill, New York, NY.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302.
- Hitchcock, C.L., Cronquist, A., 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle, WA.
- Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80, 1892–1907.
- Johnson, W.C., Burgess, R.L., Keammerer, W.R., 1976. Forest overstory vegetation and environment on the Missouri River floodplain in North Dakota. *Ecol. Monogr.* 46, 59–84.
- Krahmer, R.L., Van Vliet, A.C., 1983. *Forest Products 210: Wood Technology and Utilization*. O.S.U. Book Stores, Inc, Corvallis, OR.
- Leopold, L.B., Wolman, M.G., Miller, J.P., 1964. *Fluvial Processes in Geomorphology*. Dover Publications, Mineola, N.Y.
- McCune, B., Grace, J.B., 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, Oregon.
- Minore, D., Zasada, J.C., 1990. *Acer macrophyllum* Pursh. bigleaf maple. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North American Hardwoods*, vol. 12, USDA Handbook. pp. 33–40.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3, 153–168.
- Owston, P.W., 1990. *Fraxinus latifolia* Benth. Oregon Ash. In: Burns, R.M., Honkala, B.H. (Eds.), *Silvics of North American Hardwoods*, vol. 12, USDA Handbook. pp. 339–342.
- Perala, D.A., Alban, D.H., 1994. Allometric biomass estimators for aspen-dominated ecosystems in the Upper Great Lakes. USDA Forest Service Research Paper NC-134: 38 (As presented in: Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. *For. Ecol. Manage.* 97, 1–24).
- Rood, S.B., Heinze-Milne, S., 1989. Abrupt downstream forest decline following river damming in southern Alberta. *Can. J. Bot.* 67, 1744–1749.
- Rood, S.B., Mahoney, J.M., Reid, D.E., Zilm, L., 1995. Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. *Can. J. Bot.* 73, 1250–1260.
- SAS Institute, 2004. JMP IN version 4.0. Cary, N.C.
- Sedell, J.R., Froggatt, J.L., 1984. Importance of streamside forests to large rivers: the isolation of the Willamette river, Oregon U.S.A., from its floodplain by snagging and streamside forest removal. *Verh. Internat. Verein. Limnol.* 22, 1828–1834.
- Shannon, C.E., 1948. A mathematical theory of communications. *Bell System Tech. J.* 27, 379–423.
- Smith, D., et al., 1995. *Willamette River Recreation Guide*. Extension Service, Oregon State University, Corvallis, Oregon, EM 8598.
- Standish, J.T., Manning, G.H., Demaerschalk, J.P., 1985. Development of biomass equations for British Columbia tree species. Canadian Forestry Service, Pacific Forestry Research Centre, Victoria, British Columbia.
- Towle, J.C., 1982. Changing geography of Willamette Valley woodlands. *Oregon Historical Q.* 83, 67–87.
- United States Forest Products Laboratory, 1974. *Wood Handbook*. U.S. Government Printing Office, Washington, D.C..
- United States Geological Survey, 2001. Peak streamflow for the Nation. USGS 14174000 Willamette River at Albany, Oregon. <http://waterdata.usgs.gov>.
- Wentz, D.A., Bonn, B.A., Carpenter, K.D., Hinkle, S.R., Janet, M.L., Rinella, F.A., Uhrich, M.A., Waite, I.R., Laenen, A., Bencala, K.E., 1998. *Water Quality in the Willamette Basin, Oregon, 1991–95*: U.S. Geological Survey Circular 1161, on line at <URL: <http://water.usgs.gov/pubs/circ1161/>>, updated June 25, 1998.