Water yield following forest–grass–forest transitions

Running head: Species changes affect water yield over time

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Abstract. Many currently forested areas in the southern Appalachians were harvested in the early 1900s and cleared for agriculture or pasture, but have since been abandoned and reverted to forest (old-field succession). Land use and land cover changes such as these may have altered the timing and quantity of water yield (*Q*). We examined 80 years of streamflow and vegetation data in an experimental watershed that underwent forest-grass-forest conversion (i.e., old-field succession treatment). We hypothesized that changes in forest species composition and water use would largely explain long-term changes in *Q*. Aboveground biomass was comparable among watersheds before the treatment (208.3 Mg ha^{-1}), and again after 45 years of forest regeneration (217.9 Mg ha^{-1}). However, management practices in the treatment watershed altered resulting species composition compared to the reference watershed. Evapotranspiration (ET) and *Q* in the treatment watershed recovered to pretreatment levels after nine years of abandonment, then *Q* became less (averaging 5.4% less) and ET more (averaging 4.5% more) than expected after the 10th year up through present day. We demonstrate that the decline in *Q* and corresponding increase in ET could be explained by the shift in major forest species from predominantly *Quercus* and *Carya* before treatment to predominantly *Liriodendron* and *Acer* through old-field succession. The annual change in *Q* can be attributed to changes in seasonal *Q*. The greatest management effect on monthly *Q* occurred during the wettest (i.e., above median *Q*) growing season months when *Q* was significantly lower than expected. In the dormant season, monthly *Q* was higher than expected during the wettest months.

Keywords*:* diffuse-porous, evapotranspiration, forest succession, paired watersheds, ring-porous, water yield

1 Introduction

Forests play a critical role in regulating hydrological processes in headwater catchments by moderating the timing and magnitude of streamflow (Burt and Swank, 2002; Chang, 2003; Ice and Stednick, 2004; Ford et al., 2011b; Vose et al., 2011). Hydrological processes in forests are particularly sensitive to disturbances that reduce tree vigor or leaf area and thus decrease evapotranspiration (ET) (Aranda et al., 2012; Edburg et al., 2012; Brantley et al., 2013). Most efforts at studying the effects of disturbance on watershed hydrology have focused on quantifying the effects of forest harvesting practices on water yield (Q) (Bosch and Hewlett, 1982; Stednick, 1996; Burton, 1997; Brown et al., 2005; Wei and Zhang, 2010; Ford et al., 2011a; Zhang and Wei, 2012; Liu et al., 2015). Reviews have shown that, in general, harvesting <20 % of the basal area shows no detectable increase in annual Q; but, Q increases thereafter as the percentage of basal area harvested increases (Bosch and Hewlett, 1982; Andréassian, 2004; Brown et al., 2005). However, recent work that aims to merge ecology of the resulting forest and species composition with traditional hydrology approaches (i.e., ecohydrology) has advanced our understanding greatly. For example, Brantley et al. (2013, 2015) showed that lasting changes in annual Q (lower) and persistent changes in peakflow (> 20%, after the most intense storms) were observed with only about a 5 % basal area loss of eastern hemlock (*Tsuga canadensis* (L.) Carrière). Brantley et al. (2013) also suggested that a change in forest composition with less evergreen hemlock relative to deciduous trees could result in an increase in Q in winter months.

Most of the Eastern U.S. forests have been harvested at least once since the late 1800s (Yarnell, 1998; Foster et al., 2003; Thompson et al., 2013; Martinuzzi et al., 2015), and many forested areas have undergone forest to agriculture land use changes, and then been abandoned to revert back to forest (i.e., abandoned agriculture or old-field succession) (Otto, 1983; Trimble et al., 1987; Wear and Bolstad, 1998; Bellemare et al., 2002; Alvarez, 2007; Thiemann et al., 2009; Ramankutty et al., 2010; Kirk et al., 2012). Land abandonment has also been prevalent and ongoing since the early 20th century in other countries (Cramer et al., 2008; García-Ruiz and Lana-Renault, 2011). Land use and land cover (LULC) changes, such as forest–grass–forest transitions, may alter the timing and quantity of Q. Because land use conversion from forests to agriculture often includes a combination of changes in vegetation composition and soil physical attributes, it is difficult to separate the effects of vegetation changes from soil changes (see reviews by Neary et al., 2009; Zimmermann et al., 2010; Houlbrooke and Laurenson, 2013, Morris and Jackson, 2016). Land cover conversion that requires heavy machinery or includes livestock grazing decreases soil infiltration and saturated hydraulic conductivity (e.g., Hassler et al., 2011; Price et al., 2011; Morris and Jackson, 2016), and can thus increase peak flow during storms, and flood frequency and severity (Reinhart, 1964; Hornbeck, 1973; Burt and Swank, 2002; Alila et al., 2009; Green and Alila, 2012). Without soil compaction and alteration of water flow pathways, forest trees typically use more water and extract water from deeper soil than shallower-rooted grasses (Zhang et al., 2001; Kulmatiski and Beard, 2013), which could result in higher ET and lower Q at the catchment scale.

Several studies have compared Q and ET of forests and pastures. Analyzing 250 catchments worldwide, Zhang et al. (2001) found that forested catchments had higher ET than grass pastures, with few exceptions. Replacing trees with grass cover generally increases Q by decreasing ET (Hibbert, 1969; Bosch and Hewlett, 1982; Farley et al., 2005), although not always (Brauman et al., 2012; Amatya and Harrison, 2016). In some basins when agricultural land use is reduced and forest cover increased, Q is unchanged, and can be explained in part by the species-specific traits in water use (e.g., deciduous vs. evergreen, and/or late season vs. early season perennial grass) (Cruise et al., 2010), and the geomorphological differences among biomes (Zhou et al., 2015).

Large differences among tree species in their leaf and canopy conductance, transpiration per unit leaf area, and whole tree water use for any given diameter exist in Eastern U.S. deciduous forests (Wullschleger et al., 2001; Ford and Vose 2007; Ford et al., 2011a). This is especially true when comparing hardwoods within diffuse-porous and ring-porous xylem functional groups (Taneda and Sperry, 2008; Ford et al., 2011a; von Allmen et al., 2015). *Liriodendron tulipifera*, a diffuse-porous species common to the eastern temperate deciduous forest biome, has among the highest transpiration rates of forest trees; while, rates of *Acer rubrum* L. and *Betula lenta* L., also common diffuse-porous species, are lower than *L. tulipifera*. However, they have relatively high transpiration rates compared to common ring-porous *Quercus* species (Ford et al., 2011a).

Few studies have examined long-term changes in catchment hydrology through a forest–grass–forest transition, with specific attention focused on species compositional changes and their effect on ET and *Q*. A treated watershed within the Coweeta Hydrologic Laboratory, western North Carolina experienced this LULC transition, and reported similar *Q* between forest and grass when the grass cover was well fertilized (Hewlett and Hibbert, 1961; Hibbert, 1969; Bosch and Hewlett, 1982; Burt and Swank, 1992). However, they did not investigate why *Q* was lower than expected after grass cover abandonment and through the early successional development of the deciduous forest. Road construction could be a contributing factor because installing temporary roads to facilitate timber harvesting can affect hydrology (Harr et al., 1975; Alila et al., 2009), but only 3.3 % of the watershed area was in temporary roads (inactive for the least 50 years). In addition, roads comprising less than 6 % of the watershed area appear not to change storm hydrographs significantly (Harr et al., 1975; Swank et al., 2001; Alila et al., 2009). In a more recent study, Ford et al. (2011b) suggested that the decline in *Q* over time could be due to a shift in the dominant tree species in the treated, old-field succession watershed.

Working in the same experimental watershed as authors above, we compared the long-term changes (1934‒2015) in: 1) aboveground biomass, leaf area index (LAI) and species and functional (xylem anatomy) group composition; 2) estimated growing season mean daily water use (DWU); 3) annual water-balance derived ET; and 4) daily, monthly, and annual *Q* between the treated, old-field succession, watershed (WS6) and nearby reference (WS14, WS18) watersheds with an emphasis on the period of reforestation. We hypothesized that: 1) a shift in species composition and their attendant DWU will largely explain long-term changes in *Q*; 2) annual *Q* would be lower in the treated WS6 through forest succession concurrent with greater DWU with additional changes in timing of *Q* due to altered species composition; and 3) monthly *Q* would be greater in the treated WS6 for wet periods (high or peak flows) and this effect would be greatest in the dormant season.

2 Materials and Methods

2.1 Study area

The study was conducted at the USDA Forest Service Coweeta Hydrologic Laboratory, a 2185 ha forested basin in the Nantahala National Forest in North Carolina, U.S. (35° 06′ N, 83° 43′ W). Climate in the Coweeta Basin is classified as marine, humid temperate (Swift et al., 1988), with mild temperature (average 12.8 °C) and ample precipitation (average 1795 mm yr^{-1}). Three watersheds (WS6, WS14 and WS18) within 1 km of one another, similar in elevation, slope, and aspect were used in this study (Table 1). WS14 and WS18 are untreated reference watersheds (Fig. 1). WS6 experienced a disturbance regime similar to forest conversion to pasture and subsequent abandonment common across the region (see below). Soils in all watersheds are moderately permeable, well-drained, moderately deep to very deep, and with a saprolite layer up to 6 m deep (Thomas, 1996).

2.2 History of disturbance

Before 1842, the Coweeta Basin was burned semiannually (Douglass and Hoover, 1988). Between 1842 and 1900, light semiannual burning and grazing continued. From 1912 to 1923 heavy logging occurred (Douglass and Hoover, 1988). Loss of American chestnut (*Castanea dentata* (Marshall) Borkh.) in the 1930s (Woods and Shanks, 1959; Elliott and Swank, 2008) was followed by loss of *Tsuga canadensis* (L.) Carrière in the 2000s (Elliott and Vose, 2011).

The disturbance regime in WS6, the treated watershed, was extensive (Table S1). In July 1941, 12% of the catchment (1.06 ha area) along the stream was cut to determine how riparian vegetation affects Q (Dunford and Fletcher, 1947). In 1958, the entire watershed was clear-cut, merchantable timber was removed, and the residue was piled and burned. In 1959, surface soil was scarified and seeded to *Festuca octiflora* grass. In 1960, the watershed was treated with a one-time application of 1100 kg ha^{-1} lime, 110 kg ha^{-1} 30-10-10 NPK and 18.4 kg ha^{-1} granular 60% potash. Between 1960 and 1965, *Kalmia latifolia* L., *Rhododendron maximum* L., and other hardwood sprouts were suppressed with spot applications of 2,4D [(2,4dichlorophenoxy) acetic acid] to maintain the watershed in grass cover (Hibbert, 1969). In 1965, the watershed was fertilized again, as above. In 1967, the grass was herbicided with atrazine [2-chloro-(4-ethylamino)-6-9-isopropylamino)-Strizine], paraquat [1,1 dimethyll 4,4 bipyridinium ion (dichloride salt)], and 2,4D [(2,4dichlorophenoxy) acetic acid] (Douglass et al., 1969), and then left undisturbed (hereafter, old-field succession). Although the grass was not cut or grazed, the lime and fertilizer amendments with attendant high productivity and nutrient uptake by the grass make these applications somewhat similar to agricultural practices. The original objectives of the conversion from forest-to-grass were to compare water use of grass versus hardwoods (Hibbert, 1969; Swank and Crossley, 1988) and to determine how conversion to grass affects discharge characteristics (Burt and Swank, 1992).

Two adjacent forested watersheds (WS14, WS18) were selected as references to provide an adequate number of sample plots (described below) for analysis of changes in vegetation. These reference watersheds with similar physiography (Table 1) are characteristic of mature, second-growth hardwood forests, and have remained unmanaged since 1923 (Swank and Crossley, 1988). We considered forest age for WS14 and WS18 since the loss of *C. dentata* presently to be > 75 years old.

2.3 Measurements

2.3.1 Vegetation

The relative importance of woody species over time was characterized with repeated tree surveys. In treated WS6, surveys were conducted in 1934, 1958, 1982, 1995 and 2012. In 1934, only five 0.08 ha permanent plots were measured along the east-side of the watershed; in all subsequent surveys, plots were placed across the entire watershed. In 1958, a pretreatment strip inventory sampled 25 % of the watershed area with 10 m wide strips approximately 40 m apart extending along transects from the ridge-top to the stream channel. This sampling method resulted in a total of 37 unequal sized plots (ranging from 0.02 to 0.14 ha), including the riparian corridor. In 1982, thirty-four 0.02 ha plots were permanently marked continuously along five transects from ridge-top to near stream; these 34 plots were re-measured in 1995 and 2012.

In reference WS14, thirty-one 0.08 ha permanent plots, were surveyed in 1934, 1969, 1988–1992 (hereafter, 1992), and 2009–2010 (hereafter, 2009). In reference WS18, eight 0.08 ha permanent plots were surveyed in 1934, 1953, 1969, 1992, and 2009.

In all watersheds and for all survey periods, diameter of woody stems ≥ 2.54 cm at breast height (DBH, 1.37 m above ground) was measured by species and recorded into 2.54 cm DBH classes. In 1934, only percent cover was recorded for the two evergreen shrubs, *Rhododendron maximum* and *Kalmia latifolia*; for this reason, we do not estimate biomass and leaf are index (LAI, m^2 of leaf area m^{-2} ground area) for these species in 1934. In all other years, stem diameters of these evergreen shrubs were measured in the same manner as the tree diameters. Median DBH values were used to calculate basal area, aboveground biomass, leaf biomass, and LAI. We used species-specific allometric equations developed on-site to estimate the aboveground biomass, leaf biomass, and LAI contribution of each species in each watershed (McGinty, 1972; Santee and Monk, 1981; Martin et al., 1998; Ford and Vose, 2007; B.D. Kloeppel, unpublished data; C.F. Miniat, unpublished data). Species nomenclature follows Kirkman et al. (2007).

2.3.2 Water yield (*Q*) and evapotranspiration (ET)

We used both chronological-pairing (i.e., corresponding to the same meteorological input) and frequency-pairing (described below) analyses to detect potential hydrologic responses of *Q* and ET to land use and land cover change. Both analyses used the paired watershed approach (Wilm, 1944; Wilm, 1949). The chronological pairing approach allowed us to create a time series of estimated change in annual *Q* and ET over the period of record and to relate these changes to both the treatment and to climate. In addition, this analysis allowed us to determine when a consistent change in *Q* began, enabling us to establish the time period of interest for the frequency pairing. The frequency pairing approach allowed us to compare the post-treatment distribution of monthly and annual *Q* to that of the pretreatment period. We used WS18 and WS6 as the reference and treatment watersheds, respectively. We did not compare WS6 to WS14 because there were gaps in the WS14 flow record in the years immediately following the grass conversion and herbicide application. For both watersheds, 5-min stream stage was used to estimate *Q* (Reinhard and Pierce, 1964; Swift et al., 1988).

We modeled WS6 annual *Q* and ET as a function of WS18, incorporating the effect of grass conversion and reforestation treatments over time. Annual *Q* was computed on a May–April water year to minimize the effects of year-to-year changes in storage, as soils are generally at their wettest by the beginning of May. The empirical chronological-pairing model was fit using PROC NLIN (SASv9.4, SAS Institure, Cary, NC) and had the following form:

$$\hat{Q}_T = a + bQ_R + eM1t1 + \left[M2c\left(h - \frac{1}{1+exp^{-t2}}\right)\right], \quad (1)$$

where,

$\hat{Q}_T$ = predicted *Q* from treated watershed WS6 (mm yr^{-1}),

Q_R = measured *Q* from reference watershed WS18 (mm yr^{-1}),

M1 = management representing grass conversion; M1 = 1 for water years between and including 1960 and 1966, M1 = 0 otherwise,

t1 = time since grass fertilization; t1 = water year – fertilization year for water years between and including 1960 and 1966 where fertilization years include water years 1959, 1961, and 1966, t1 = 0 otherwise,

M2 = management representing reforestation after grass conversion; M2 = 1 for water years greater than or equal to 1967, M2 = 0 otherwise,

t2 = time since reforestation after grass conversion; t2 = water year – 1967 for water years greater than or equal to 1967, t2 = 0 otherwise,

a, *b*, *c*, *e*, *h* are fitted parameters.

This overall modeling approach has been used in prior studies to assess the impact of forest management on *Q* (Ford et al., 2011b; Kelly et al., 2016). The $a + bQ_R$ term in EQ1 reflects the relationship between reference and treatment watersheds assuming no treatment. The increasing linear *Q* response ($eM1t1$ term in EQ1) accounts for the decline in annual grass production after fertilization and water use as noted by Hibbert (1969). The $M2c\left(h - \frac{1}{1+exp^{-t2}}\right)$ term in EQ1 accounts for the exponential decline in *Q* as the forest regenerates that has been observed in numerous paired watershed experiments (Swank et al., 1988).

As in Ford et al. (2011), we define the *Q* treatment response, D_Q, as the difference between the observed *Q* in the treated watershed (Q_T) and that predicted by the model assuming no treatments had taken place ($\hat{Q}_T$)

$$\boldsymbol{D_Q} = Q_T - \left(\hat{Q}_T;\ M1, M2 = 0\right). \qquad (2)$$

The proportion of the variability explained by the model was quantified using the ratios of the error-to-total sum of squares and the total-to-error degrees of freedom as:

$$R^2_{adjusted} = 1 - \frac{SS_E}{SS_T} \times \frac{df_T}{df_E}. \qquad (3)$$

Parameter estimates were interpreted as statistically significant at $\alpha = 0.05$. Observed annual ET was computed as precipitation (P) – Q_T while expected ET with no treatment was computed as P - $\hat{Q}_T$, both assuming the largely impermeable bedrock underlying the basin that results in negligible deep groundwater losses (Douglass and Swank, 1972). Watershed P was estimated using a nearby eight inch (20.3 cm) National Weather Service standard rain gauge, SRG 96 (Laseter et al., 2012). The ET treatment response, D_{ET}, is then:

$$\boldsymbol{D}_{\mathbf{ET}} = [P - Q_T] - \left([P - \hat{Q}_T];\ M1, M2 = 0\right) \qquad (4).$$

2.3.3 Frequency-pairing flow distributions

We used the frequency-pairing method (Alila et al., 2009; Brantley et al., 2015) to detect differences in frequency between observed and predicted annual and monthly Q after treatment. Briefly, frequency-pairing is an analytical method that quantifies differences in observed and predicted Q parameters based on the probability of occurrence of a given Q (or flow at a given probability) rather than based on occurrence at a discreet time (i.e., chronological-pairing). This accounts for rainfall amount and antecedent soil conditions. We used pre-treatment Q during water years 1939–1941, 1948–1951, and 1956–1958, to estimate the expected cumulative distribution functions (CDFs, F_{Y}) for observed and predicted Q in the treatment watershed using the linear regression equation:

$$\hat{Y}_{\mathrm{i}} = b_0 + b_1 X_{\mathrm{i}}, \qquad (5)$$

where, X_{i} is the observed Q in the reference watershed for period i (day of year) and $\hat{Y}_{\mathrm{i}}$ is the expected Q for the treatment watershed under undisturbed conditions for the same period. We used PROCMODEL (SAS v9.3, SAS Institute, Cary, NC) to predict monthly post-treatment *Q* in the treatment watershed from May 1979–Apr 2015 and annual post-treatment *Q* for water years 1980–2015. To model monthly *Q*, we separated the data by calendar month and created twelve separate regression equations. Using separate regression equations for each month helped account for variations in paired watershed *Q* relationships among months and helped to distinguish differences in effects among seasons.

Observed and predicted *Q* values were then plotted as an estimate of the probability of occurrence for ranked event $Y_{(i)}$ during any time period *i*. The exceedance probability, 1-*p*, was estimated for each period using the equation:

$$1 - F_Y\left[\hat{\mathrm{Y}}_\mathrm{i}\right] = \frac{m-0.40}{n+0.20}, \qquad (6)$$

where, *m* was the rank for a given flow and *n* was the total number of flow periods in the distribution. This function provided an empirical estimate of the quantile for a given flow value (Cunnane, 1978; Stedinger et al., 1993). Confidence limits for each predicted flow at each probability of occurrence were estimated as:

$$Y_m \pm\, z_{1-\frac{\alpha}{2}}\sqrt{(Var_1\,[Y_m]\, +\, Var_2\,[Y_m])}. \qquad (7)$$

We used a pair of Monte-Carlo simulations to estimate the variability associated with the predictive uncertainty in equation (Var_1), and the uncertainty associated with the sampling variability at each rank (Var_2). For these analysis, we used 1000 iterations for each simulation. We used the raw, expected post-treatment values from equation (5) to correct for the loss of variability in the upper tails of the distribution (Alila et al., 2009). The CDFs were then used to construct flow duration curves to assess changes in untransformed *Q* at monthly and annual intervals by comparing the change in magnitude for a given probability or the change in probability for a given magnitude (Alila et al., 2009; Green and Alila, 2012; Brantley et al., 2015).

2.3.4 Growing season daily water use (DWU)

Plant water loss was estimated by scaling up sap flux measurements of numerous species and stem diameter sizes at Coweeta Hydrologic Laboratory (Ford and Vose, 2007; Ford et al., 2011b; Brantley, et al. 2013; Miniat, unpublished) using methods outlined in Ford et al. (2011a). We fitted the observed growing season mean daily water use (DWU, kg day^{-1}) to stem DBH (cm) using a power function of the form:

$$\mathrm{DWU} = b_0 * \mathrm{DBH}^{b1} \qquad (8)$$

Species were grouped into xylem functional types (diffuse-porous, ring-porous, semi-ring porous, evergreen shrub, or tracheid) and growing season DWU models were developed for each xylem functional type. For example, *Carya* spp. have semi-ring porous xylem; *Quercus* spp. and *Oxydendron arboreum* have ring-porous xylem; and *Betula lenta*, *Liriodendron tulipifera*, and *Acer rubrum* have diffuse-porous xylem (Table S2). Because *R. pseudoacacia* behaves more like a diffuse-porous species, its measured values of DWU and DBH were combined with the diffuse-porous model. Even though *Robinia pseudoacacia* has ring-porous xylem, it is isohydric (i.e., maintaining stable leaf water potentials as soil water potentials drop, Klein, 2014) and has higher DWU than *Quercus* or *Carya* (Miniat and Hubbard, unpublished). For the two understory evergreen species, *Kalmia latifolia* and *Rhododendron maximum*, we applied the mean DWU value from 16 instrumented shrubs because DWU models based on DBH alone provided limited predictive power (Table 2). We estimated growing season mean plot DWU by modeling DWU by functional type and vegetation surveys by diameter for all watersheds. We did not estimate DWU for the 1934 survey, when *C. dentata* was most abundant, because most of the trees had been affected by chestnut blight compromising their functional xylem.

3 Results

3.1 Vegetation dynamics

Prior to treatment, species composition and aboveground biomass among the watershed were similar (Fig. 2). In 1934, aboveground biomass was comparable among the treated WS6 and references WS14 and WS18 averaging 200 Mg ha^{-1} (p = 0.706) (Fig. 2a, Table S3). Biomass declined in WS6 (99.51 Mg ha^{-1}) from 1934 to 1958 prior to conversion to grass, and in WS18 (148.42 Mg ha^{-1}) from 1934 to 1953 (Table S3). The decline in biomass and LAI between 1934 and the 1950s was primarily due to the loss of *Castanea dentata* (Fig. 2a–c). In 1934, *C. dentata* occupied from 40–54 % of the biomass and 29–43 % of the LAI across the three watersheds (Fig. S1).

The grass cover in the treated watershed was highly productive, but following the herbicide treatment (i.e., old-field succession), early-successional vegetation rapidly established (Fig. S1a). During the five years when WS6 was maintained in grass, biomass ranged from 5.67 to 7.30 Mg ha^{-1}. In 1968, one year after cessation of treatment, the aboveground biomass was 3.92 Mg ha^{-1} in WS6. At that time, the one year old field was dominated by *Erechitites hieracifolia* (L.) Raf., *Phytolacca americana* L., *Eupatorium* spp., *Equisetum arvense* L. and had remnants of *Festuca octiflora*. In the years between 1968 and 1982, WS6 was rapidly colonized by *Robinia* *pseuodoacacia* and *Liriodendron tulipifera* (Fig. S1a); whereas the most abundant species in the reference watersheds in the years following the loss of *C. dentata* (1969 to 2010s) were *Quercus* spp. and *Acer rubrum* (Fig. S1b–c; Tables S4‒S6).

Forest composition following grass cover was biased towards tree species with deep functional sapwood and diffuse-porous xylem. In 1934, all watersheds were dominated by species with semi ring-porous (*C. dentata* and *Carya*) or ring-porous (*Quercus*) xylem, accounting for more than 80 % of the aboveground biomass (Fig. 3a–c) and 80 % of the LAI (Tables S4–S6). Although species with semi ring-porous xylem declined in all watersheds over time, the increase in species with diffuse-porous xylem was greater in the treated watershed compared to reference watersheds (Fig. 3a–c). As the young forest developed following grass herbicide and abandonment, species with diffuse-porous xylem and *R. pseuodoacacia* dominated forest biomass, while species with ring-porous xylem were only 2.7 %. By 2012, 93 % of vegetation in the treatment watershed was comprised of species with diffuse-porous xylem (Fig. 3a), while the reference watersheds were about half of the species with ring-porous xylem (Fig. 3b–c).

3.2 Water yield (*Q*) and evapotranspiration (ET)

The forest‒grass‒forest treatment of WS6 resulted in significant effects on *Q* over time. Models of annual *Q* explained more than 98% of the variability in *Q* over the period of record. Initial harvesting increased *Q* by 99 mm (10.5 % above the expected *Q*) in 1960 (Fig. 4), and *Q* remained higher than expected during the grass conversion period except in 1959, 1961, and 1966 when grass production was highest due to fertilizer application. The largest treatment effect occurred in 1967 when herbicide was applied to the watershed, resulting in a *Q* increase of 259 mm (31 % above the expected *Q*) (Fig. 4). *Q* remained higher than expected for approximately nine years after the herbicide treatment as the vegetation re-established. Beginning in 1977 and continuing through 2015, *Q* was less than expected in 32 of 35 years (Fig. 4), suggesting that the new forest used more water (i.e., had higher ET) than expected had it not undergone treatment. Since 1980, on average, annual *Q* decreased by 6.1 %, ranging from a *Q* increase in 1981 of 30 mm (+5.5%) to a decrease of 142 mm (16%) in 2003. ET increased by 4.5 % on average relative to what was expected in the absence of management (Fig. S2).

3.3 Changes in flow distribution

In addition to the forest-grass-forest treatment changing the amount of Q, it also fundamentally changed the distribution of Q, with the most pronounced changes at the height of the growing and dormant seasons. The annual and monthly *Q* relationships between the reference and treatment watersheds for the pre-treatment period were highly significant (annual, $n = 10$, $r^2 = 0.97$, $p < 0.001$; monthly, $n = 10$, $r^2 = 0.94$, $p < 0.001$) using the frequency-pairing method. Annual *Q* was unchanged at low and high probabilities of non-exceedance (<10 %), but was lower in some years between the 30 % and 60 % probability of non-exceedance (Fig. 5a). Monthly *Q* was higher than expected at high probability of non-exceedance in February (Fig. 5b); whereas, monthly Q was lower than expected at the high probability of non-exceedance in July (Fig. 5c). Median monthly *Q* was lower than expected for only Jan (-14.8%) and May (-13.4%) (Table 3). At wetter periods (above median *Q*), monthly *Q* was lower than expected for several months and immediately following the growing season (Jun–Oct, Dec; Table 3); whereas, for Feb–Apr, monthly *Q* was higher than expected. At drier periods (below median *Q*), February, March and September had lower than expected monthly *Q* (Table 3). No significant changes in monthly *Q* distributions were observed in November.

3.4 Daily water use (DWU)

Growing season DWU differed among species for any given DBH largely dependent on xylem anatomy (Table 2, Fig. 6). For example, DWU for a for a tree 50 cm DBH could be 6.5 times higher with diffuse-porous xylem compared to ring-porous xylem (Fig. 5). *Liriodendron tulipifera*, *Betula lenta* and *Nyssa sylvatica* had the highest DWU; *Acer rubrum* and *Carya* were intermediate; and *Quercus alba*, *Q. montana*, and *Q. rubra* had the lowest estimated DWU compared to all other species (Ford et al., 2011b). *Robinia pseudoacacia* had higher DWU than *Quercus* or *Carya* (Miniat and Hubbard, unpublished). Models based on DBH and xylem anatomy explained 55–88 % of the variability in DWU among tree species (Table 2). For the evergreen understory species, however, DBH explained little variation in DWU, even though the standard errors were quite low.

Mean growing season DWU for each catchment increased over time, but the treated watershed showed the greatest increase (Fig. 7a). In the 2010s, the 45 year-old forest in WS6 had 25-43 % higher DWU than the > 75 year-old reference forests (Fig. 7a–d), despite lower leaf area than the reference watersheds at that time (Fig. 2c). In reference WS14, tree species with diffuse-porous xylem contributed 48–63 % of the total water use between 1969 (age 35) and 2009 (age 75+), while evergreen shrubs contributed 20–23 %, and tree species with ring-porous xylem contributed 13 % or less to the total water use (Fig. 7c). Since the grass cover was abandoned in WS6, tree species with diffuse-porous xylem alone have contributed more than 90 % of the total daily water use in that watershed (Fig. 7b).

4 Discussion

We hypothesized that a shift in species composition and the resulting shift in DWU would largely explain long-term changes in *Q* in the treated watershed as the forest regenerated following grass abandonment. We found that forest species composition in the treated watershed shifted from dominance by species with ring-porous xylem prior to grass conversion to species with diffuse-porous xylem through old-field succession. With this major shift in species composition, DWU increased from 1982 to 2012 in the treated watershed, and it was much higher than that in the older reference watersheds. These changes in species composition and DWU correspond with the long-term trend in lower than expected *Q* over that time period. Seasonal variation in *Q* helped to explain this long-term pattern.

4.1 Vegetation dynamics

Species composition has changed dramatically in the treated watershed through old-field succession following the forest-grass-forest transition. Prior to conversion to grass (1958), the forest was dominated by *Quercus montana* and *Q. coccinea*, similar to the reference watersheds at that time. After the grass was herbicided, and the forest was allowed to reestablish, the forest shifted to dominance by *Liriodendron tulipifera* and *Robinia pseudoacacia*. Other studies have found that shade-intolerant *R. pseudoacacia* and *L. tulipifera* respond and grow rapidly following clearcutting or other disturbances that create large canopy gaps (Elliott and Swank, 1994; Elliott et al., 1997, 1998; Shure et al., 2006; Boring et al., 2014). During grass dominance all woody species were eliminated with spot herbicide application. This treatment killed stump sprouts, and during forest succession recruitment favored small, wind-dispersed seeds, and discriminated against large-seeded and slow growing species such as *Quercus*, *Carya*, *Tilia,* and *Aesculus* (Elliott et al., 1997, 2002). Aboveground biomass approached pretreatment levels after 45 years of forest growth; however, LAI remained lower than that of the pretreatment or reference watershed conditions. The lower LAI could be attributed to the differences among species in the ratio of leaf area per total aboveground biomass and crown structure; where, shade intolerant *R. pseudoacacia* and *L. tulipifera* have lower ratios and concentrate foliage to the uppermost crown more than intermediate shade-tolerant *Quercus* (Kato et al., 2009).

Many studies have investigated forest growth following harvesting (e.g., Palik et al., 2012; Boring et al., 2014; Loftis et al., 2014; Stanturf et al., 2014; Boggs et al., 2016), and the hardwood species composition that succeeds following harvest depends largely on the severity of disturbance, i.e., partial harvest, retention harvest or clearcutting, as well as the geographical region (Halpin and Lorimer, 2016). In northern Appalachian forests, *Prunus pensylvanica* and *Betula papyrifera* are common pioneer species that assume early dominance following clearcutting (Hornbeck et al., 2014). In central Appalachian forests, *Prunus serotina*, *Acer rubrum*, *Betula lenta*, and *Fagus grandifolia* dominate following extensive harvests (Kochenderfer, 2006; D′Amato et al., 2015). *Robinia pseudoacacia* and *L. tulipifera*, two species that recruit and grow rapidly after clearcutting, are much more abundant in the southern Appalachians (Elliott and Vose, 2011; Boring et al., 2014) than in the central Appalachians

(Kochenderfer, 2006), and are absent in the northern Appalachians (Campbell et al., 2007; Hornbeck et al., 2014).

4.2 Species effects on water yield (*Q*) and evapotranspiration (ET)

We found that annual *Q* declined and ET increased through old-field succession relative to the time prior to the grass conversion. After 1980, 13 years following herbicide application, *Q* was consistently lower than expected for the next 35 years. *Q* was reduced by 6.5% averaged over this time period; however, in 16 of those years, *Q* was greatly reduced (>50 mm, 9.2 %). In 2003 and 2015, *Q* was reduced by 142 mm (16 %) and 113 mm (17 %), respectively. This supports our hypothesis that changes in ET and *Q* have occurred as a result of a shift in species composition. We also found that species effects were seasonal and influenced certain parts of the flow regime.

The range of changes in *Q* after treatment suggests that species composition affects storage and use of water under a wide range of precipitation conditions that play out over monthly and annual scales. For example, in 2003, when the decrease in *Q* was greatest (-142 mm; 16%), *P* was 6% greater than the long-term (1939-2015) average but this followed four years of below average *P*. Average *P* for 1999-2002 was 23% below the long-term average. In this case, the vegetation in the old-field succession watershed may have used more of the available water in 2003, following the dry period, than the vegetation in reference watersheds. As a result, less of the available water served to refill soil storage in the treated watershed compared to the reference watershed, resulting in a larger predicted decrease in *Q* in 2003. In 1981 when *Q* was higher than expected (+30 mm; 5.5%), *P* was 29% lower than the long-term average but this followed the second highest annual P in 1980 (+27% greater than the 1939-2015 average). Much of the excess rainfall occurred at the end of the 1980 water year and the beginning of water year 1981. Precipitation during March and April of water year 1980, and May of water year 1981 was 123%, 35%, and 39% greater than the long-term (1939-2015) average for those months, respectively. Given that the Q for the treated watershed was higher than expected in wetter months (those above median Q) of the dormant season, these wet months resulted in a higher than expected annual Q.

Our monthly analysis showed that changes in ET and Q varied seasonally. First, changes in monthly distribution of Q suggest that old-field succession and the consequent species changes have lowered streamflow during the growing season during wetter months. We observed that Q was lower than expected in September during both drier (below median Q) and wetter periods suggesting that changes in soil storage at the end of the growing season highly influences base-flow. Others have found that forest clearcutting had a longer-lasting influence on streamflow distribution, even when annual Q returned to baseline conditions within a few years (Burt et al., 2015; Kelly et al., 2016).

Second, changes in monthly distribution of Q suggest that there is a potential for increased frequency and severity of high flows in dormant season months under wet conditions. This could be particularly concerning during severe tropical storms. However, for the Appalachian region most tropical storms occur later in the year (Sep–Dec) (Holland and Webster, 2007; Smith et al., 2011). Interestingly, we found lower than expected Q during wetter periods for Sep–Dec months. If timing of large storms remains unchanged, then shifting species composition from those that have conservative water use (i.e., ring-porous xylem) to those that are less conservative (i.e., diffuse-porous xylem) could mitigate the effects of high flows during large storms.

The observed changes in monthly *Q* during the dormant season indicate a likelihood of soil saturation during the wettest periods. Higher than expected *Q* in the dormant season is likely a result of lower ET and higher soil moisture at that time of year (Berghuijs et al., 2014; Burt et al., 2015), rather than reduced infiltration capacity. For example, in an earlier study, Burt and Swank (1992) reported that the dead grass was not removed following herbicide application on the treated watershed and so the infiltration capacity remained high throughout 1967 and 1968. More likely the higher than expected *Q* in the dormant season is due to the lack of evergreen species in the treated watershed. Where evergreen species are a component of forested watersheds, they can affect ET and *Q* in the dormant season (Brantley et al., 2013, 2015); they transpire during dormant season months as long as environmental conditions are suitable (Ford and Vose, 2007; Ford et al., 2011a; Brantley, unpublished data) and they intercept precipitation during the dormant season because they retain their foliage. Even though evergreens (shrubs + tracheids) were a relatively small component (13.8 % of total aboveground biomass) of the old-field succession watershed before treatment, after treatment there were no evergreen shrubs due to the severity of the treatment. Yet, they remain a component (6.0 % and 15.9 % for WS14 and WS18, respectively) of the reference watersheds. Thus, evergreen species reduce soil moisture storage and have the potential to mitigate spring flooding because of their contribution to ET and their location within riparian zones (Brantley et al., 2015).

Our results demonstrate that species changes largely explain the decreasing trend in *Q* following old-field abandonment based on modeled growing season DWU over time and enable us to assess the effects of forest structure and species composition on *Q*. For example, the estimates of DWU (Fig. 6) are consistent with the differences in temporal patterns of *Q* between the old-field succession WS6 and reference watersheds (Fig. 3). The mean DWU in WS6 was greater in 1995 than DWU in the reference watersheds in 1969 or 1992, suggesting that *Q* in WS6 became less than expected between these years due to altered DWU. Similarly, mean DWU in the 45 year-old old-field succession WS6 was greater still in 2012 than the > 75 year-old reference watersheds, WS14 or WS18, in 2010. Indeed, *Q* was consistently less than expected during this period, and was significantly less in 32 of the 35 years (including 1995, 2010, and 2012).

Few studies have examined the consequence of shifts in hardwood species composition on the hydrologic cycle (Swank et al., 2014; Caldwell et al., 2016). Changes in forest composition, structure and age as well as climate will interact to induce long-term changes in *Q* from forested mountain watersheds (von Allmen et al., 2015; Caldwell et al., 2016). We found stronger and longer lasting decreases in annual and monthly *Q* through old-field succession, than found by clearcutting alone followed by forest succession (Reinhart, 1964; Hornbeck, 1973; Swank et al., 2001, 2014; Troendle et al., 2001; Adams and Kochenderfer, 2014; Hornbeck et al., 2014). For example, researchers at the Fernow Experimental Forest in West Virginia examined changes in annual *Q* following clearcutting (Adams and Kochenderfer, 2014); there, the initial increase in *Q* returned to pretreatment levels within 3-4 years. In another treated watershed (WS7) in Coweeta that was allowed to regenerate naturally after the clearcut, there was only one year when observed *Q* was significantly lower than predicted (Swank et al., 2014).

The observed changes in monthly and annual *Q* for the treated WS6 were largely a result of a rapid response of co-dominant species with less conservative transpiration rates (Wullschleger et al., 2001; Ford et al., 2012; Boggs et al., 2015; Brantley et al., 2015). Under similar environmental conditions, both *L. tulipifera* and *R. pseudoacacia* have much higher daily water use than species with ring-porous and semi ring-porous xylem, such as *Quercus* and *Carya* (Ford et al., 2011b; Vose et al., 2016a, b). Overall, we estimated that growing season daily water use increased significantly following old-field abandonment, and it was much higher in the 45 year-old treated watershed than the > 75 year-old reference watersheds.

5 Conclusions

Our long-term results are relevant to land areas that are currently in pasture and those that have reverted back to forests. In many parts of the world, pastureland and cropland area have increased since the 1990s as natural landscapes have been converted to agricultural ecosystems (e.g., Scanlon et al., 2007; Rodriguez et al., 2010); and in other areas agricultural land has been abandoned (see review Rey Benayas et al., 2007). In general, grass pastures transpire less water and have lower interception loss than forests resulting in greater *Q* for this LULC type (e.g., Wang et al., 2008; Holdo and Nippert, 2015). In the forest-grass-forest watershed, for two of the five years when the watershed was in grass cover, *Q* was equivalent to the pre-conversion hardwood forest, while for the other three years *Q* was greater under grass cover. Fertilizer application in two of the five years resulted in high grass productivity (Hewlett, 1961; Hewlett and Hibbert, 1966; Burt and Swank, 1992) such that LAI was maximized allowing for ET similar to that of the reference forested watershed. *Q* increased initially once herbicide was applied to the grass, quickly returned to expected levels, and then declined relative to expected levels as the abandoned old-field was allowed to regenerate to forest.

We found that within a deciduous forest, species identity matters in terms of how much precipitation leaves the watershed as ET vs. *Q*. Through old-field succession, the treated watershed was dominated by water demanding species with higher DWU than the pretreatment forest. We demonstrate that a shift in tree species composition from dominance by species with ring-porous xylem to dominance by species with diffuse-porous xylem can increase DWU, and in turn, produce a long-term reduction in *Q*.

Even within unmanaged watersheds, hydrologic parameters are not stationary (*sensu* Milly et al., 2008; Burt et al., 2015) and subtle changes in species composition can influence *Q*, particularly in dry years (Caldwell et al., 2016). Species-specific ecohydrological models (e.g., Novick et al., 2016) are increasingly vital in predicting long-term changes in ET and *Q* (Sun, et al. 2016; Vose et al., 2016a, b). If drought frequency and severity increase as expected (Allen et al., 2010; Ayres et al., 2014; Peters et al., 2015; Swain and Hayhoe, 2015), then understanding the interaction of land use, species and climate change on water resources will become even more important in the future (Grant et al., 2013; Clark et al., 2016; Kelly et al., 2016; Vose et al., 2016b). As previously outlined as a critical research need (Vose et al., 2016b), our results provide an example of scaling DWU from tree-level, plots, and small watersheds in order to understand the species-specific influences on water balance and streamflow dynamics in diverse Eastern U.S. deciduous forests.

The Supplement related to this article is available online at doi:-supplement.

Data availability. All data in this manuscript is archived at USDA Forest Service, Southern Research Station, Coweeta Hydrologic Laboratory, Otto, NC, 28763.

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Table 1. Characteristics of treated (WS6) and reference (WS14, WS18) watersheds at the Coweeta Hydrologic Laboratory in Otto, NC, USA. Mean annual precipitation (*P*) and water yield (*Q*) based on data collected over water years (WY, May–Apr) from 1934 to 2015.

		Watersheds		
Characteristic	Units	6	14	18
Area	ha	9.0	61.03	12.46
Mean elevation	m	824	878	823
Mean basin slope	%	50	50	55
Aspect		NW	NW	NW
Year of first complete flow record	WY	1939	1938	1938
Nearest rain gauge		SRG41	SRG41	SRG96
Mean precipitation (*P*)	mm yr^{-1}	1843	1843	2031
Mean water yield (*Q*)	mm yr^{-1}	866	997	1021
Mean evapotranspiration ($ET = P - Q$)	mm yr^{-1}	978	845	1010
Q/P		0.47	0.54	0.50

Table 2. Summary of growing season daily water use (DWU, kg day^{-1}) models for each xylem functional group as a function of stem diameter at breast height (DBH, cm); DWU = b_0 * DBH^{b_1}.

Xylem Group	N	Min DBH (cm)	Max DBH (cm)	b_0	b_1	Adjusted R^2	SE of estimate
Diffuse-porous	95	7.4	61.8	0.1428	1.7676	0.70	30.3
Evergreen Shrub	16	5.3	16.3	0.6445	0.7002	0.00	2.5
Ring-porous	38	23.9	86.7	0.2392	1.1488	0.55	9.1
Semi ring-porous	18	20.2	55.7	0.0009	2.8557	0.88	8.8
Tracheid	116	9.5	67.5	0.0005	2.8411	0.73	8.6

Table 3. Relative changes in monthly water yield (*Q*) for different parts of the cumulative distribution function for the period May 1979 to Apr 2015 for the treated WS6 using the frequency-pairing method. Lower and Higher denote direction and significance ($p < 0.05$) of change, NS = not significant.

Month	Change in Median Monthly *Q* (%)	Change in *Q* below the median *Q*	Change in *Q* above the median *Q*
Jan	Lower (-14.8)	NS	NS
Feb	NS	Lower	Higher
Mar	NS	Lower	Higher
Apr	NS	NS	Higher
May	Lower (-13.4)	NS	NS
June	NS	NS	Lower
Jul	NS	NS	Lower
Aug	NS	NS	Lower
Sep	NS	Lower	Lower
Oct	NS	NS	Lower
Nov	NS	NS	NS
Dec	NS	NS	Lower

Figures

Figure 1. Map of the Coweeta Basin with treated WS6 and reference (WS14, WS18) watersheds with rain gauges, weirs, and vegetation plots.

Figure 2. Mean (±SE bars) **(a)** aboveground biomass, **(b)** leaf biomass, and **(c)** leaf area index (LAI) for the treated WS6 and reference (WS14, WS18) watersheds over time.

Figure 3. Percent (±SE bars) aboveground biomass for the xylem functional groups (diffuse-porous, ring-porous, semi-ring porous, tracheid, and evergreen shrub) in the **(a)** treated WS6, **(b)** reference WS14, and **(c)** reference WS18 over time.

Figure 4. Changes in water yield ($Q,\ D = Q_T - \left(\hat{Q}_T;\ M1, M2 = 0\right)$) for the treated WS6 over time (bars). Solid lines are the standard errors of the mean prediction. We used the paired-watershed approach with WS18 as the reference. The year of harvest, conversion to Kentucky-31 fescue grass (*Festuca octiflora*) cover, fertilize, herbicide, and abandonment to allow forest regeneration are denoted by dashed lines.

Figure 5. Changes in the cumulative distribution function (CDF) expressed as historic probability of non-exceedance for **(a)** annual water yield (Q), and monthly Q for **(b)** February and **(c)** July. * ($p < 0.05$) and ** ($p < 0.01$) denote years in the distribution functions when Q was significantly lower or higher than predicted.

Figure 6. Growing season daily water use of tree species by xylem functional group (diffuse-porous, ring-porous, semi-ring porous, evergreen shrub and tracheid) and DBH (diameter at 1.37 m above ground).

Figure 7. **(a)** Mean (±SE bars) growing season daily water use (DWU) versus forest age in the treated WS6 and reference (WS14, WS18) watersheds; **(b)** DWU versus forest age in treated WS6 by xylem functional group (diffuse-porous, ring-porous, semi-ring porous, evergreen shrub,

and tracheid); **(c)** DWU versus forest age in reference WS14 by xylem functional group; and **(d)** DWU versus forest age in reference WS18 by xylem functional group.

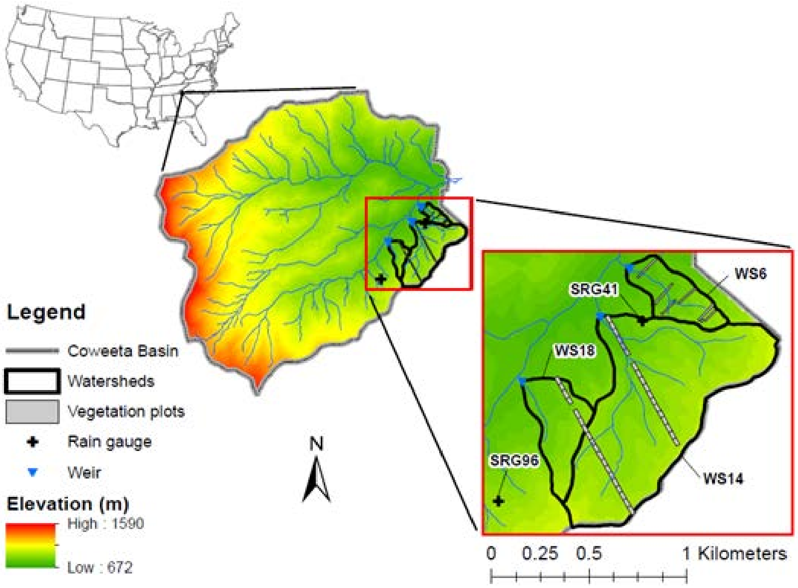


Figure 1

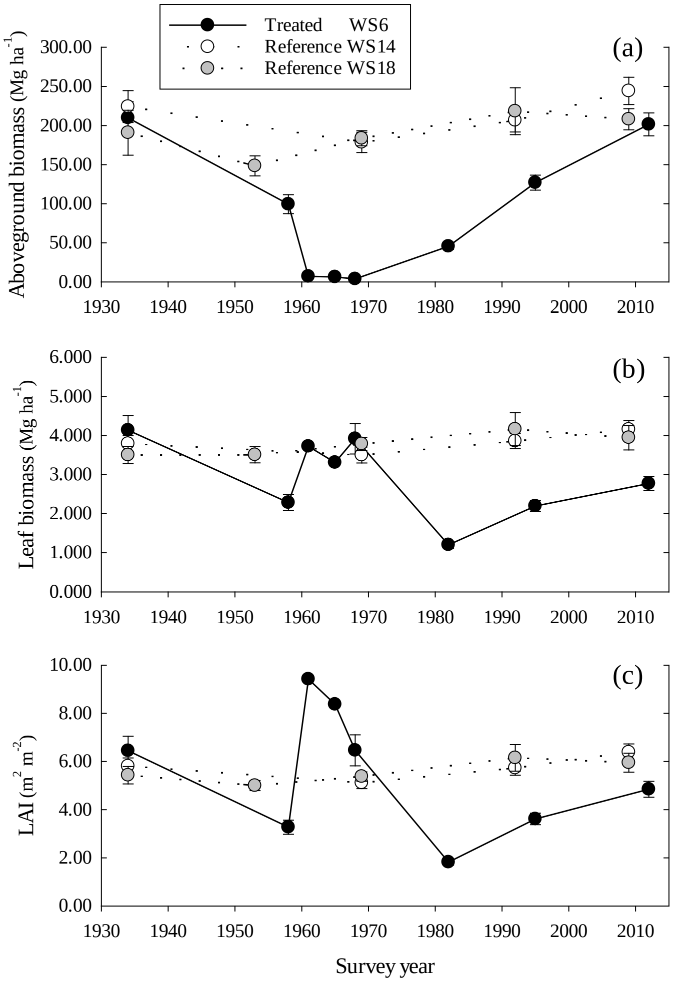

Treated WS6
Reference WS14
Reference WS18
(a)
Aboveground biomass (Mg ha^{-1})
300.00
250.00
200.00
150.00
100.00
50.00
0.00
(b)
Leaf biomass (Mg ha^{-1})
6.000
5.000
4.000
3.000
2.000
1.000
0.000
(c)
LAI (m^2 m^{-2})
10.00
8.00
6.00
4.00
2.00
0.00
1930
1940
1950
1960
1970
1980
1990
2000
2010
Survey year

Figure 2

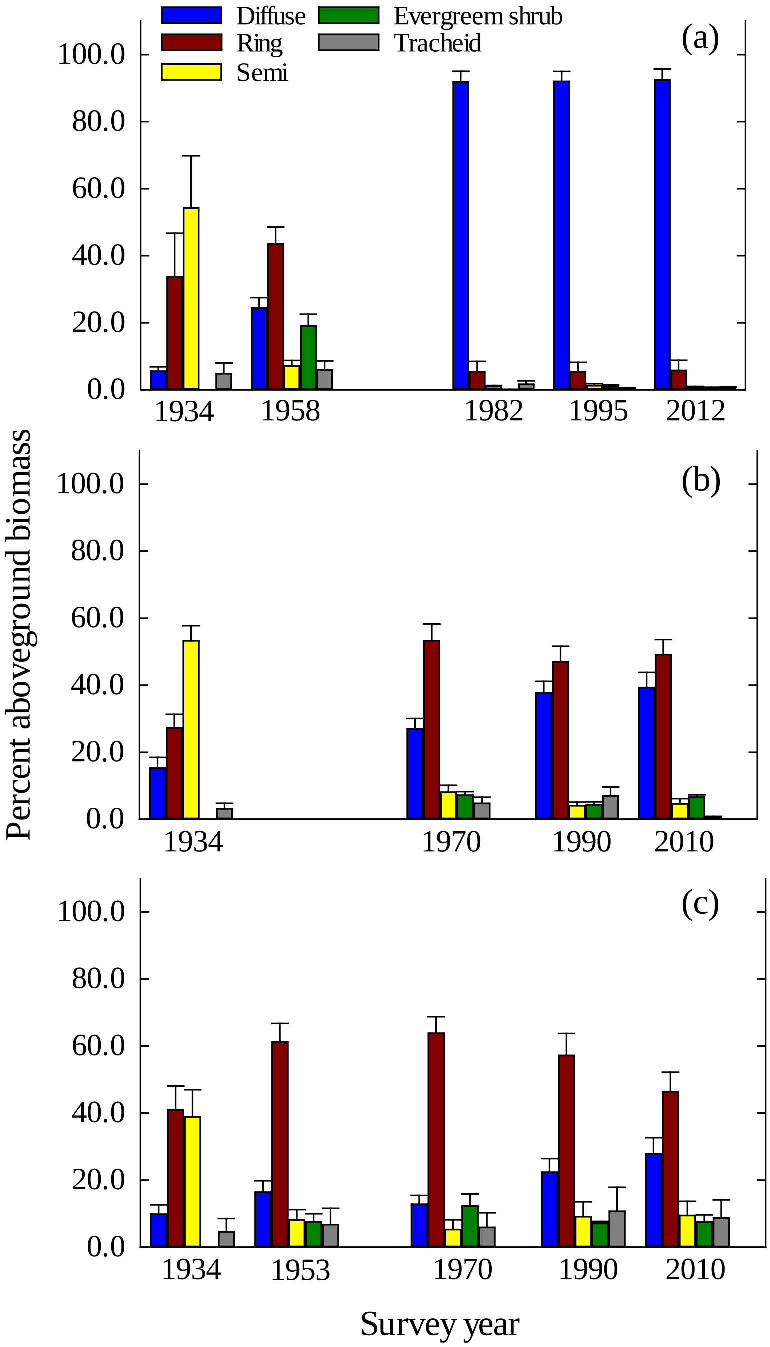

Diffuse
Ring
Semi
Evergreem shrub
Tracheid
(a)
(b)
(c)
100.0
80.0
60.0
40.0
20.0
0.0
1934
1958
1982
1995
2012
1934
1970
1990
2010
1934
1953
1970
1990
2010
Percent aboveground biomass
Survey year

Figure 3

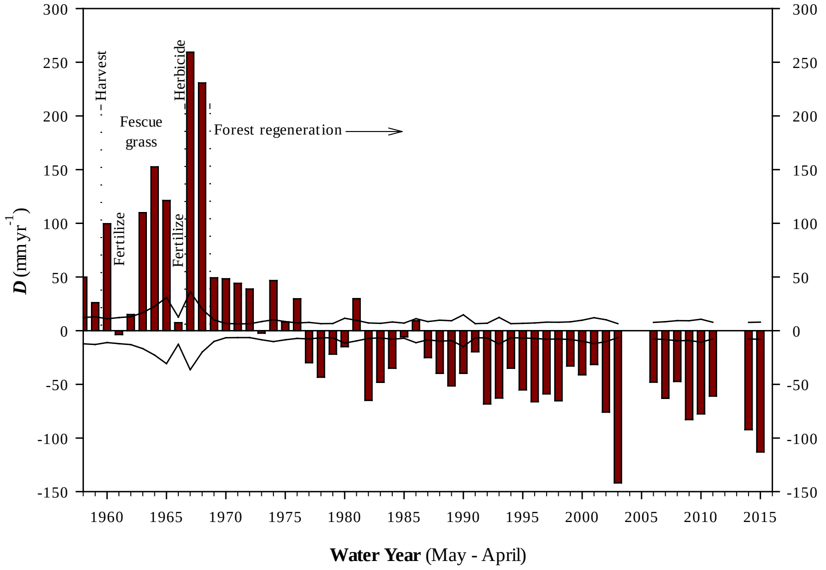

300
250
200
150
100
50
0
-50
-100
-150
Harvest
Fertilize
Fescue grass
Herbicide
Fertilize
Forest regeneration
D (mm yr^{-1})
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
Water Year (May - April)

Figure 4

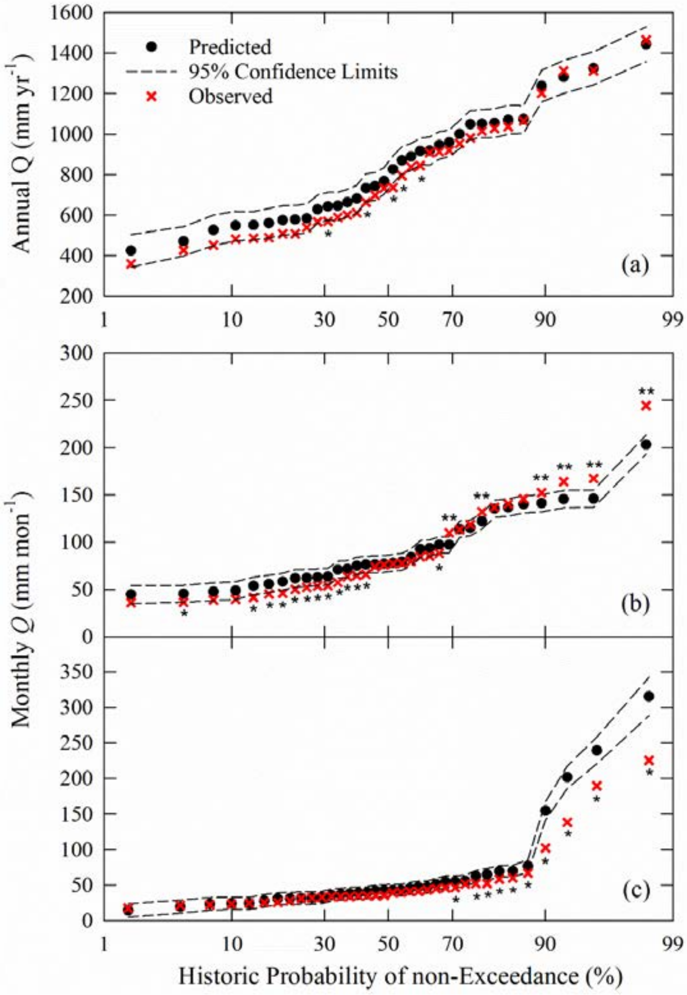
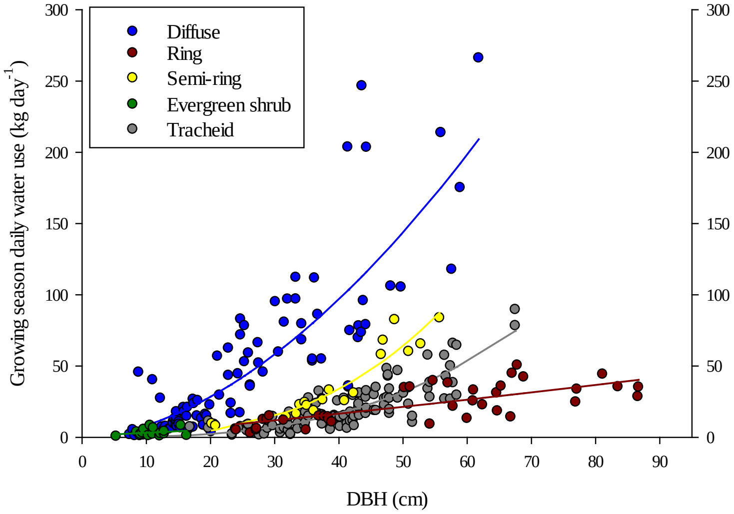

Annual Q (mm yr^{-1})
1600
1400
1200
1000
800
600
400
200
Predicted
95% Confidence Limits
Observed
(a)
Monthly Q (mm mon^{-1})
300
250
200
150
100
50
0
(b)
350
300
250
200
150
100
50
0
(c)
1
10
30
50
70
90
99
Historic Probability of non-Exceedance (%)

Figure 5



Diffuse
Ring
Semi-ring
Evergreen shrub
Tracheid
Growing season daily water use (kg day^{-1})
DBH (cm)
0
50
100
150
200
250
300
0
10
20
30
40
50
60
70
80
90

Figure 6

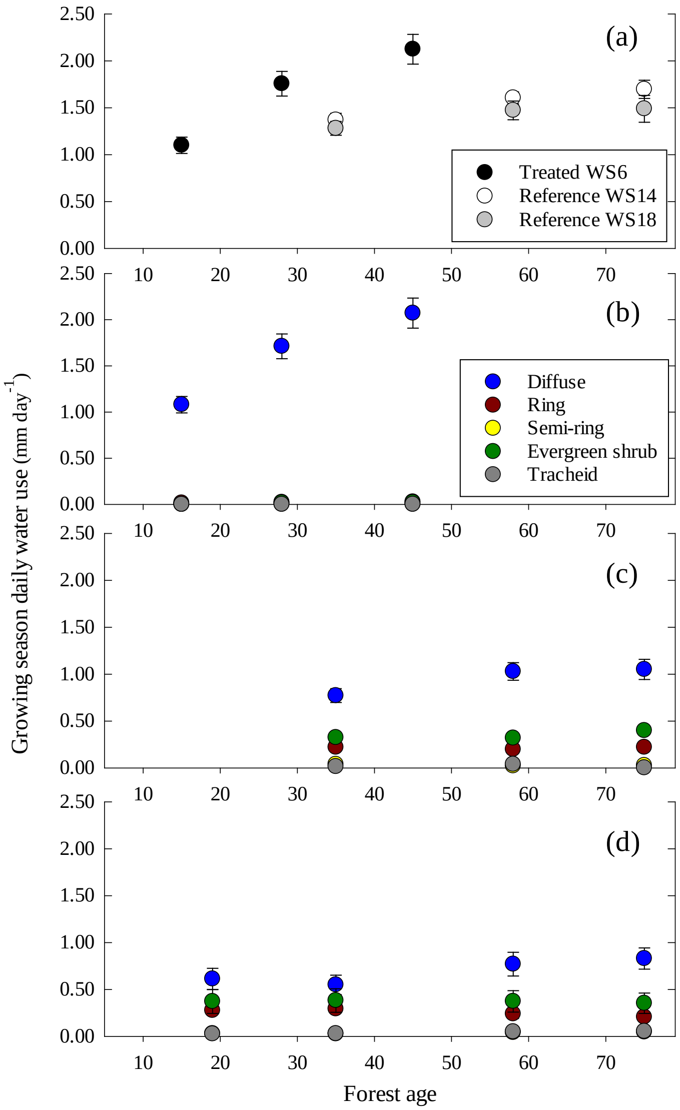

(a)
Treated WS6
Reference WS14
Reference WS18
(b)
Diffuse
Ring
Semi-ring
Evergreen shrub
Tracheid
(c)
(d)
Growing season daily water use (mm day^{-1})
Forest age
0.00
0.50
1.00
1.50
2.00
2.50
10
20
30
40
50
60
70

Figure 7