

Thirty-five-year timber harvesting disturbance effects on composition and biomass of *Nyssa-Taxodium* forested wetlands, southwest Alabama, USA

Cora Every

Virginia Polytechnic Institute and State University

Michael Aust (✉ waust@vt.edu)

Virginia Polytechnic Institute and State University

David R. Carter

Virginia Polytechnic Institute and State University

T. Adam Coates

Virginia Polytechnic Institute and State University

Erik B. Schilling

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Abstract

Thirty-five years post-harvest, effects of harvest disturbances upon tree composition and aboveground biomass were evaluated in a *Nyssa aquatica* (water-tupelo)-*Taxodium distichum* (baldcypress) bottomland. The study site, along the Tensaw River, is within the Mobile-Tensaw River Delta in southwest Alabama. Nine replications of four disturbances were evaluated: no harvest reference (REF), clearcutting with helicopter removal (HELI), HELI combined with skidder extraction simulation (SKID), and HELI combined with broadcast spray (glyphosate) of sprouts and seedlings for two years (GLYPH). Thirty-five years post-treatment, species, diameter at breast height (DBH; 1.37 m) and total tree height were measured at monumented sample plots and converted to aboveground biomass. Clip plots were installed for herbaceous and woody stems shorter than DBH. Results indicate that HELI and SKID treatments remain on a trajectory to produce species composition and volume similar to REF. GLYPH lacked adequate coppice regeneration and regenerated from seedbanks and flood and wind disseminated seed, thus the treatment has succeeded from an herbaceous freshwater marsh to an open woodland/savanna community. The GLYPH treatment emphasizes the importance of coppice for rapid tree regeneration and the need for coppice success on sites having altered hydrology. This research further demonstrates the capacity for long-term recovery of forested wetland ecosystems following harvest. Furthermore, several site/stand factors favored stand regeneration, including adequate initial stocking of species capable of stump sprouting, intact hydrology with annual sediment deposits, shrink-swell soils, nearby seed sources and flood tolerances of original species acted collectively to favor rapid recovery from both HELI and SKID disturbances.

Introduction

Passage of the Federal Water Pollution Control Act of 1972 and subsequent federal and state programs within the United States have increased understanding of the ecosystem services provided by forested wetlands (Dahl and Allord 1996; Schilling et al. 2019). Globally, Mitsch et al. (2015) identified over 25 ecosystem services provided by wetlands that could be grouped as provisioning immediate needs (e.g., food, water), regulating ecosystem services such as water purification, providing cultural ecosystem services such as recreation, and supporting ecosystem services that maintain nutrient cycling and productivity. Recognition of the importance of ecosystem services and policy shifts were fortuitous as wetland areas across the United States are estimated to have declined by approximately 50% since European settlement (Dahl 2006), while global losses have been estimated to be between 33% (Hu et al. 2017) and 87% (Davidson 2014). Multiple anthropogenic disturbances are credited with wetland losses, including agricultural conversion, drainage, urbanization, stream damming and channelization efforts, and transportation infrastructure projects (Dahl and Allord 1996). During the five decades since enactment of the Clean Water Act, both federal and state programs and legislation have shifted wetland policy from exploitative to sustainable management practices (Dahl and Allord 1996; Schilling et al. 2019).

Forested wetlands are diverse and can be classified as alluvial or nonalluvial (e.g., bogs, fens, wet mineral flats, pocosins, Carolina bays). Alluvial forested wetlands are known by a variety of names including riparian forests, floodplain forests, and bottomland hardwoods. Ecosystem services provided by these alluvial forests are diverse and include nutrient cycling, fiber production, sediment trapping, streambank stabilization, thermal protection, and provision of diverse wildlife habitat (Kellison and Young 1997; Mitsch et al. 2015). Society benefits tremendously from the flood attenuation, water quality protection, and wildlife habitat services provided by alluvial forests, and income-producing activities, such as timber harvesting.

There is a considerable body of knowledge regarding harvesting effects on forest soils and recovery, particularly in upland forests. McEachran et al. (2021) reviewed the direct and indirect effects of forest harvesting on both erosion and sediment yield and concluded that increases in erosion and sediment yield and hydrologic shifts in surface and subsurface flow are commonly associated with harvesting, particularly in the absence of appropriate best management practices (BMPs). Picchio et al. (2021) reviewed nearly 200 studies that evaluated forest harvesting disturbances on water and sediment and concluded that the effects and duration of harvest disturbances can be reduced by application of currently recommended forestry BMPs. The majority of forest harvest disturbances across all sites in the southeastern United States involve ground-based disturbances, usually skidding and skid trails. DeArmond et al. (2021) reviewed 121 studies evaluating harvest skid trail disturbances and recovery in boreal, temperate, and tropical regions and concluded that most skid trails recovered slowly and had disturbance effects that persisted for two to five decades.

Conversely, several authors have reviewed the ecological impact of timber harvesting within riparian forested wetlands and generally concluded that harvesting is compatible with maintaining ecosystem services and has relatively minor and short-term impacts (Wigley and Roberts 1997; Hutchens et al. 2004). Minimizing harvesting impacts, however, requires that the hydrology remain relatively intact (Sun et al. 2001; Slye et al. 2020), sites have sufficient regeneration sources to facilitate rapid recovery (Lockaby et al. 1997), appropriate BMPs are implemented (Aust et al. 2017), and suitable harvesting technology is utilized (Stokes and Schilling 1997).

During forest harvesting operations, maintenance of hydroperiods is crucial. Hydroperiods profoundly influence ecological functions within bottomland hardwoods through multiple mechanisms (Hupp 2000; Busbee et al. 2003; Hunter et al. 2008). Hydroperiods affect periodicity and depths of flooding, thus controlling sediment inputs from upland sources as well as sediment transport from streams during overbank flooding. Sediment inputs are important for protecting water quality, adding nutrients, and potentially offsetting subsidence or sea level rise effects. Hydroperiods influence the soil reduction-oxidation process and subsequently affect nutrient and chemical cycling, including soil nitrogen and carbon. Hydroperiods also affect the vegetation capable of regenerating on sites due to influences on seed dispersal, germination, and survival. Thus, bottomland hardwoods with long hydroperiods tend to favor species tolerant of flooding. Furthermore, within an individual floodplain, microtopographic features are created by hydroperiod patterns and differential sediment deposition (e.g., natural levees, old stream

channels, sloughs, oxbows), or disturbance-created features (e.g., windthrow pits and mounds) can influence species composition and forest structure (Hodges 1997).

Major sources of regeneration include seed from residual stems, adjacent stands, soil seed bank, and seeds transported by floodwaters, stump sprouts, seedling sprouts, advance regeneration, and root sprouts (Meadows and Stanturf 1997). Problems with regeneration in bottomland hardwoods can occur where hydroperiods have been altered so that the site no longer suits the hydrologic requirement of the regeneration, where animal predation and plant competition are severe (Slye et al. 2020), or on sites that have experienced exploitative harvesting practices, leaving few desirable species on the site (Kellison and Young 1997).

Best management practices for bottomland hardwoods are similar to those for upland sites (Aust and Blinn 2004), but the BMPs for bottomlands also recognize the lower soil strengths for supporting wheeled traffic and associated harvesting challenges (Stokes and Schilling 1997). Commonly used BMPs include provision of streamside management zones to filter waters leaving the site, minimizing rutting effects by utilizing appropriate forest operations, such as lower ground pressure equipment (e.g., wide-tired skidders), avoiding ground skidding (e.g., helicopter harvesting), or utilizing temporary access corridors reinforced with logs or panels (e.g., shovel or mat logging) (Aust 1994; Anderson and Lockaby 2011; Aust et al. 2017).

Additionally, concerns exist that harvest disturbances may negatively affect soil physical and chemical properties due to compaction, churning, or puddling of soils during wet site conditions, which have been reported following harvesting on saturated soils (Greacen and Sands 1980). Compaction can negatively affect soil bulk density and soil mechanical resistance, limiting root growth (Goutal et al. 2013). Churning can reduce soil macroporosity, further reducing soil, air, and water movement in already reduced soil conditions. Puddling can result in crusting of soil surfaces, adding an additional impediment for gas exchange (Horn et al. 2004; Aust et al. 1995, 1998). Harvest traffic has been found to negatively alter soil physical properties and subsequently influence the survival and productivity of wetland forests (Neaves et al. 2017). Aerial systems have been used in an attempt to reduce ground traffic disturbances (e.g., helicopter removal) as compared to the high levels of disturbance associated with tracked and wheeled skidding (Stokes and Schilling 1997).

Bottomland hardwoods have been altered in species composition and biomass due to repeated, exploitative harvests (i.e., high grades); however, research has shown that wetland forests' ecological functions and timber harvesting can coexist when the harvesting is done sustainably (Kellison and Young 1997; Schilling et al. 2019). Many studies document positive regeneration responses in the initial years following harvests. (Meadows and Stanturf 1997; Hutchens et al. 2004) However, there are few long-term studies of forested wetland regeneration (Schilling et al. 2019).

Clearcutting silvicultural systems, due to advantages associated with increased light available for species intolerant or intermediately tolerant of shade and logistical operations, are commonly applied to bottomland hardwoods and have been used to successfully regenerate species of oak, baldcypress, and

water tupelo (Kellison and Young 1997; Aust et al. 2020). Successful regeneration generally requires the presence of advance regeneration and adequate stump sprouting potential (Kellison and Young 1997, Meadows and Stanturf 1997; Perison et al. 1997). Baldcypress and water tupelo stands are often dense and flooded and may be lacking in advance regeneration (Meadows and Stanturf 1997). Furthermore, surface water conditions are often high following harvesting due to reduced transpiration demands, anthropogenic alteration to the hydroperiod, or beaver impoundments (Slye et al. 2020; King and Keim 2019).

The literature clearly recognizes that poorly executed harvests in bottomland hardwoods can negatively affect future species composition and productivity. However, there are few long-term studies that evaluate long-term disturbances within bottomland hardwoods. The goal of this study, conducted 35 years post-harvest, is to provide a long-term investigation of a range of disturbances on species composition and aboveground biomass in wetland ecosystems in a *Nyssa-Taxodium* (tupelo-cypress) wetland.

Materials And Methods

Site History and Condition

The study site is located on the western bank of the Tensaw River within the larger Mobile-Tensaw River Delta (MTRD) in southwestern Alabama (Fig. 1). The deltaic river system is formed below the confluence of the Tombigbee and Alabama Rivers and the entire watershed of the system contains approximately 11 million ha (Curtis et al. 1973). The easternmost river, the Tensaw River, is one of three large rivers flowing through the MTRD parallel to the Middle and Mobile Rivers. The general area was visited by the naturalist William Bartram during the late 1700s and he described the extensive *Nyssa* (tupelo) and *Taxodium* (baldcypress) forests of the area. Records indicate that this tupelo-cypress forest has experienced at least three previous timber harvests, including float logging during the late 1700s and mid-1800s as was common throughout the MTRD (Mader 1990). Residual massive cypress stumps with girdle scars also confirm float logging occurred (Aust et al. 2006). The study site was harvested again during the 1915–1918 period with pull-boat cable yarding operations. These ground-based cable yarding activities created numerous linear channels where stems were dragged toward the river, with remnants of these pull-boat “runs” still visible within every treatment area across the site (Aust et al. 2006).

These previous harvest operations produced a two-aged stand. In 1986 (study initiation), the majority of stems were approximately 70 years of age in response to the pull-boat harvest activities. Widely dispersed, large and old trees, established during the float logging period in the 1860s, were approximately 130 years old. Additionally, six very large (> 190 cm DBH) old-growth *T. distichum* (baldcypress) stems were found within the entire research area and these trees were assumed to be remnants of the precolonial forest (all hollow, no exact ages). The preharvest measurements within all treatment areas found that the site was dominated by water tupelo (85% of stems), followed by baldcypress (12%) and lower and midstory species comprised of *Fraxinus profunda* (pumpkin ash) and *F. caroliniana* (Carolina ash) (Aust et al. 2006).

The alluvial site typically floods in late fall through the spring months; however, flooding may occur during any month. Kidd et al. (2015) correlated on-site hydrograph measurements with long-term U.S. Army Corps of Engineer hydrograph records from the nearby Barry Steam Plant and reported that the site floods approximately 120 days per year, with flooding dominating during winter and spring. Soils within the study site were predominantly very poorly drained Levy series (silty clay loam, fine, mixed, superactive, acidic, thermic Typic Hydraquent), which contains montmorillonite clays with shrink-swell properties (McKee et al. 2012; Aust et al. 2006). The average annual precipitation of this area is 1600 mm yr^{-1} which is evenly distributed throughout the year, with the exception of hurricane season (Riccio et al. 1973). The region is subtropical and has average January temperatures between 6° and 16° C and average July temperatures between 24° and 33° C. Due to the long-term nature of this project, which has had multiple measurements, additional details regarding the study site and methods used during investigations between pre-treatment and stand age 25 years are available in multiple sources (Aust et al. 1989, 1990, 1991, 1997, 1998, 2006; Mader et al. 1989a, b; Aust and Lea 1991, 1992; Gellerstedt and Aust 2004; Gellerstedt et al. 2002; McKee et al. 2012, 2013; Kidd et al. 2015).

Treatments

Nine replications of four treatments were installed with each treatment replication measuring $60 \times 60 \text{ m}$ (0.86 ha) (Fig. 2). Additional buffers and access corridors were also included so that the entire disturbance treatments equaled 25 ha. All disturbance treatments were installed in fall 1986 using chainsaw felling. These treatments were located adjacent to a non-disturbed reference area (REF) that was measured before treatment installation, and treatment areas were found to have similar harvest history, hydrology, soil, and vegetation (Aust and Lea 1992). A Bell 205 helicopter was used to fly all felled, merchantable stems from all disturbance treatments to riverbank landings for barge transport (Aust 1989). This minimally trafficked level of disturbance comprises the HELI treatment. A Franklin 105 rubber-tired cable skidder (SKID) was used to simulate ground-based mechanical removal by dragging logs across approximately 50% of the designated plots. This trafficking treatment created an average rutted area of 52% with an average rut depth of 30 cm. The third treatment involved herbicide application and did not represent any applied silvicultural treatment; rather, it was superimposed upon the HELI treatments to investigate the importance of initial regeneration success from coppice and the existing seedbank to future stand regeneration. Rodeo™, the wetland approved formulation of glyphosate (GLYPH), was applied via backpack sprayers as a broadcast herbicide treatment to prevent coppice regeneration of woody and herbaceous species. This treatment was applied twice during the first two growing seasons and represents a severe disturbance that is not a silvicultural practice. All treatments within the harvest area were installed in $60 \times 60 \text{ m}$ plots. We originally suspected distance to the river to impact treatments, so treatments were installed on a grid system having three 3×3 Latin squares for a total of nine replications per treatment (Fig. 2). Due to logistical restraints regarding the HELI treatment safety, the REF area was located adjacent to the disturbance treatments and nine pseudoreplications having the same distance from the river were installed. The majority of overstory trees within the adjacent reference plots were 103 years old in 2021. Additional information about the original treatments and installation can be found in Aust (1989) and Mader (1990).

Field Methods

All measurements were based on the most recent remeasurement of the site at stand age 23 years (McKee et al. 2012). Sampling occurred during two weeks in June 2021. Within each of the 36 treatment areas, there is a monumented 0.02-ha circular sampling plot for overstory trees in the center of the treatment area. Each permanent plot center was found and remeasured. Overstory tree measurements included all live stems ≥ 9.1 cm DBH at 1.37 m aboveground. Species, DBH (collected with d-tape; cm), total height (collected with Truepulse laser hypsometer, Laster Technology, Inc.; m), and apparent origin (seed vs. sprout) were recorded for all overstory trees. Lowerstory stems were measured in 0.004-ha circular plots nested within the overstory plots. Lowerstory measurements included all live stems < 9.1 cm that were at least 1.37 m tall. Species, DBH, total height, and apparent stem origin were recorded for all lowerstory stems. Ground flora vegetation measurements consisted of three 0.5-m² clip plots (1.5 m² per overstory plot) located 3.6 m from plot center at azimuths of 120, 240, and 360 degrees. Each clip plot was established with a 0.5 $\times$ 0.5 m sampling frame, and all herbaceous and woody plants < 1.37 m tall were severed with clippers at their root collar and placed in labeled plastic bags for subsequent drying and weighing.

Lab Methods

Ground vegetation collected within the 0.5 $\times$ 0.5 m sampling frame was transported to Virginia Tech (Blacksburg, VA). All samples were transferred to paper bags and then placed in drying ovens for over 36 hours at 66° C. After drying, samples were weighed to the nearest 0.01 g and adjusted for paper bag weights.

Statistical Analyses

We conducted statistical comparisons on species presence, stem densities (trees per hectare), DBH, heights, and biomass (kg) for the overstory and lowerstory data, as well as the total biomass. Analyses were performed for all species and strata combined. To estimate dry weight, aboveground biomass of the overstory and lowerstory species within each plot, equations obtained from Jenkins et al. (2003) were used based on species-specific parameters (Table 1).

Table 1
Volume equations used to estimate aboveground biomass from Jenkins et al. (2003). Units for dry weight biomass (bm) are in kg and diameter at breast height (DBH; 1.37m) in cm.

Species	Equation
<i>Acer rubrum</i>	$bm = \text{Exp} (- 1.9123 + 2.3651 \ln DBH)$
<i>Fraxinus caroliniana</i>	$bm = \text{Exp} (- 2.4800 + 2.4835 \ln DBH)$
<i>Nyssa aquatica</i>	$bm = \text{Exp} (- 2.4800 + 2.4835 \ln DBH)$
<i>Salix nigra</i>	$bm = \text{Exp} (- 2.2094 + 2.3867 \ln DBH)$
<i>Taxodium distichum</i>	$bm = \text{Exp} (- 2.0336 + 2.2592 \ln DBH)$

Although the original experimental design was arranged in Latin squares, only nonsignificant differences along the river have been established over time. Therefore, the data were analyzed as a randomized complete block design having nine replications of the three disturbance treatments and the control. Data were examined for normality with Shapiro's goodness of fit test and then an analysis of variance was conducted at $\alpha = 0.05$. If significant differences were detected at the treatment level, a Tukey's HSD mean separation test was used to differentiate these responses. In instances where data were not normally distributed, a Kruskal Wallis nonparametric test was used to evaluate among-treatment differences and a Steel-Dwass post-hoc test was used to examine mean differences between treatments. All tests were done using JMP Pro 16.

Results And Discussion

Across all disturbance treatments, five tree species comprised 98% of the total species stem count: baldcypress, water tupelo, Carolina ash, black willow (*Salix nigra*), and red maple (*Acer rubrum*) (Table 2). Water tupelo, Carolina ash, and baldcypress stems within the HELI and SKID treatments were primarily stump sprouts, while nearly all overstory stems within the GLYPH treatments were seed origin (data not shown). Both pre-harvest and 35-year post-treatment measurements indicated that overstories of all treatments were dominated by three species: water tupelo, Carolina ash, and baldcypress. A fourth species, black willow, became established within all of the disturbance treatments. Species present and dominant at stand ages 2 (Aust et al. 1990), 7 (Aust et al. 1997), 16 (Gellerstedt and Aust 2004), and 23 (McKee et al. 2012) were also similar. Early black willow dominance, however, clearly declined in HELI and SKID, but did not decline in GLYPH. Prior to the initial harvest, black willow was not present on the sites, but this pioneer species became established in the first two years following harvest (Mader 1990).

Table 2

Average overstory stem density (stems ha⁻¹) of species at 35 years listed in order of prevalence. Letters indicate significant differences for a given species among treatments, as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
———— (stems ha ⁻¹ $\pm$ standard error) ————					
<i>Nyssa aquatica</i>	785 ($\pm$ 83) a	1065 ($\pm$ 83) a	192 ($\pm$ 83) b	297 ($\pm$ 83) b	< 0.0001
<i>Fraxinus caroliniana</i>	456 ($\pm$ 49) a	264 ($\pm$ 49) b	148 ($\pm$ 49) b	137 ($\pm$ 49) b	0.0002
<i>Taxodium distichum</i>	121 ($\pm$ 47)	220 ($\pm$ 47)	110 ($\pm$ 47)	104 ($\pm$ 47)	0.2790
<i>Salix nigra</i>	11 ($\pm$ 32) b	27 ($\pm$ 32) b	165 ($\pm$ 32) a	–	0.0036
All species	1538 ($\pm$ 88) a	1702 ($\pm$ 88) a	851 ($\pm$ 88) b	544 ($\pm$ 88) b	< 0.0001

Average overstory stem density for all species did not differ between SKID (1702 stems ha⁻¹) and HELI (1538 stems ha⁻¹), but both were greater than the understocked GLYPH (851 stems ha⁻¹) and mature stocked REF (544 stems ha⁻¹). Water tupelo had the greatest stem density within the overstory across all treatments and comprised 62% of SKID (1065 stems ha⁻¹), approximately 50% of HELI and REF (786 stems/ha and 193 stems ha⁻¹, respectively), and approximately 22% of GLYPH (297 stems ha⁻¹) (Table 2). Interestingly, since the 23-year remeasurement in 2010 by McKee et al. (2012), water tupelo stem density in the overstory of SKID decreased by 28%. According to McKee et al. (2012), black willow dominated GLYPH and has since decreased by 44% in stems ha⁻¹.

The lowerstory density data show little treatment effects except at the cumulative species level (p value < 0.008, Table 3). The HELI and SKID average above 2700 stems ha⁻¹, followed by the GLYPH. The REF has fewer understory stems (525 ha⁻¹) as compared to all disturbance treatments. Within the disturbance treatments there is more red maple regeneration, which was not present within the lowerstory of the REF, and black willow is nonexistent. Within all disturbance treatments Carolina ash, bald cypress, and water tupelo are abundant within the lowerstory.

Table 3

Average lowerstory stem density of species at 35 years listed in order of prevalence. Letters indicate significant differences for a given species among treatments as indicated by a Wilcoxon Nonparametric comparisons test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (stems ha ⁻¹ ± standard error) —————					
<i>Fraxinus caroliniana</i>	1840 (± 365)	1694 (± 414)	988 (± 1095)	494 (± 414)	0.1096
<i>Acer rubrum</i>	1236 (± 422)	1730 (± 422)	803 (± 211)	–	0.2071
<i>Taxodium distichum</i>	680 (± 405)	865 (± 331)	247 (± 811)	–	0.2667
<i>Nyssa aquatica</i>	247 (± 86)	346 (± 54)	247 (± 121)	–	0.5724
All species	2773 (± 404) a	2938 (± 404) a	1518 (± 458) b	525 (± 428) c	0.0008

Average overstory stem diameter was similar among all three treatments. HELI, SKID, and GLYPH treatments averaged 18.6, 19.4, and 18.7 cm, respectively. However, the species with the greatest DBH in SKID and HELI was water tupelo (22.1 cm and 22.9 cm, respectively), and black willow in GLYPH (28.7 cm) (Table 4). The increased DBH of black willow can be attributed to the lower stem density of GLYPH which allowed individual trees to receive increased water, light, and nutrients (McKee et al. 2012). Evaluation of the lowerstory stem diameters (Table 5) and heights (Table 7) indicates similar overall growth within the HELI and SKID followed by lowerstory stems of smaller diameter and heights within both GLYPH and REF.

Table 4

Average overstory diameter of species at 35 years. Letters indicate significant differences for a given species among treatments as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (cm ± Standard Error) —————					
<i>Nyssa aquatica</i>	22.9 (± 2.3) b	22.1 (± 2.3) b	14.0 (± 2.3) c	48.3 (± 2.3) a	< 0.0001
<i>Taxodium distichum</i>	14.9 (± 5) b	17.1 (± 5) b	18.1 (± 5) b	37.3 (± 5) a	0.0109
<i>Fraxinus caroliniana</i>	11.9 (± 0.4)	11.0 (± 0.5)	11.8 (± 0.6)	13.2 (± 0.7)	0.4269
<i>Salix nigra</i>	9.3 (± 5.6)	20.9 (± 5.6)	28.7 (± 5.6)	–	0.0644
All species	18.6 (± 2.6) b	19.4 (± 2.5) b	18.7 (± 3.5) b	36.9 (± 4.4) a	0.0093

Table 5

Average lowerstory individual tree diameter at breast height (1.37 m) of species at 35 years. Letters indicate significant differences among treatments for a given species as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (cm $\pm$ standard error) —————					
<i>Acer rubrum</i>	4.6 ($\pm$ 0.8)	6.1 ($\pm$ 0.7)	4.5 ($\pm$ 0.5)	–	0.1350
<i>Fraxinus caroliniana</i>	6.0 ($\pm$ 0.2) a	5.4 ($\pm$ 0.2) ab	3.6 ($\pm$ 0.9) bc	3.6 ($\pm$ 0.5) c	< 0.0001
<i>Nyssa aquatica</i>	3.7 ($\pm$ 1.2)	7.4 ($\pm$ 0.6)	6.1 ($\pm$ 1.6)	–	0.0648
<i>Taxodium distichum</i>	4.3 ($\pm$ 0.6)	4.9 ($\pm$ 0.4)	1.8 ($\pm$ 1.9)	–	0.2742
All species	5.7 ($\pm$ 0.3) a	5.7 ($\pm$ 0.2) a	3.2 ($\pm$ 0.5) b	3.5 ($\pm$ 0.8) ab	0.0005

Mean heights were very similar for overstory species among treatments (SKID = 13.1 m, HELI = 13.0 m, and GLYPH = 11.3 m) and approximately 9 m less than REF (22.2 m). The species with the greatest overstory heights within SKID, HELI, and REF was water tupelo (14.3 m, 14.6 m, and 27.5 m, respectively), and black willow in GLYPH (15.5 m) (Table 6).

Table 6

Average overstory individual tree heights of species at 35 years. Letters indicate significant differences among treatments for a given species as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (m $\pm$ standard error) —————					
<i>Fraxinus caroliniana</i>	10.8 ($\pm$ 0.7)	10.1 ($\pm$ 0.7)	8.0 ($\pm$ 0.7)	10.1 ($\pm$ 0.7)	0.0532
<i>Nyssa aquatica</i>	14.6 ($\pm$ 1.2) b	14.3 ($\pm$ 1.2) b	8.0 ($\pm$ 1.2) c	27.5 ($\pm$ 1.2) a	< 0.0001
<i>Salix nigra</i>	4.6 ($\pm$ 2.6) b	9.1 ($\pm$ 2.6) b	15.5 ($\pm$ 2.6) a	–	0.0210
<i>Taxodium distichum</i>	9.2 ($\pm$ 2.4) b	11.0 ($\pm$ 2.4) b	9.1 ($\pm$ 2.4) b	23.0 ($\pm$ 2.4) a	0.0004
All species	13.0 ($\pm$ 1.1) b	13.1 ($\pm$ 1.1) b	11.3 ($\pm$ 1.5) b	22.2 ($\pm$ 1.9) a	0.0013

Table 7

Average lowerstory individual tree heights of species at 35 years. Letters indicate significant differences among treatments for a given species as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (m $\pm$ Standard Error) —————					
<i>Acer rubrum</i>	—	—	—	—	—
<i>Fraxinus caroliniana</i>	7.1 ($\pm$ 0.5) a	7.1 ($\pm$ 0.6) a	4.1 ($\pm$ 1.5) ab	4.2 ($\pm$ 0.6) b	0.0021
<i>Nyssa aquatica</i>	5 ($\pm$ 1.2)	7.4 ($\pm$ 0.8)	9.1 ($\pm$ 1.8)	—	0.2153
<i>Taxodium distichum</i>	4.2 ($\pm$ 0.4)	4.9 ($\pm$ 0.3)	3.7 ($\pm$ 0.7)	—	0.2554
All species	6.7 ($\pm$ 0.4) a	6.6 ($\pm$ 0.4) a	3.7 ($\pm$ 0.6) b	4.2 ($\pm$ 1.1) ab	0.0025

Overstory SKID and HELI biomass were not significantly different (Table 10). However, both treatments were dominated by water tupelo (252.5 Mg ha⁻¹ and 213.9 Mg ha⁻¹, respectively) (Table 8). Carolina ash did differ significantly between these treatments, with HELI values (22.7 Mg ha⁻¹) more than double SKID values (9.0 Mg ha⁻¹) (Table 8). Black willow was the dominant species in GLYPH (Table 8). Ground flora was also highest in GLYPH (Table 10).

Table 8

Average aboveground biomass of overstory species at 35 years. Letters indicate significant differences among treatments for a given species as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (Mg ha ⁻¹ $\pm$ Standard Error) —————					
<i>Fraxinus caroliniana</i>	22.7 ($\pm$ 3.6) a	9.0 ($\pm$ 3.6) ab	6.3 ($\pm$ 3.6) b	7.5 ($\pm$ 3.6) b	0.0107
<i>Nyssa aquatica</i>	213.9 ($\pm$ 30.9) b	252.5 ($\pm$ 30.9) b	39.4 ($\pm$ 30.9) c	423.6 ($\pm$ 30.9) a	< 0.0001
<i>Salix nigra</i>	40.6 ($\pm$ 18.3)	33.0 ($\pm$ 11.6)	47.7 ($\pm$ 8.6)	—	0.6073
<i>Taxodium distichum</i>	18.3 ($\pm$ 15.7) b	32.8 ($\pm$ 15.7) ab	25.3 ($\pm$ 15.7) ab	84.3 ($\pm$ 15.7) a	0.0228
All species	272.8 ($\pm$ 31.4) b	317.2 ($\pm$ 31.4) b	137.0 ($\pm$ 31.4) c	515.6 ($\pm$ 31.4) a	< 0.0001

Aboveground biomass (overstory, lowerstory, and ground flora) was greatest in REF plots (517.9 Mg ha⁻¹), followed by SKID (339.3 Mg ha⁻¹), HELI (293.5 Mg ha⁻¹), and then GLYPH (142.3 Mg ha⁻¹) (Table 10). SKID treatments contained more total biomass than HELI plots at age 35 years, which is consistent with values found by McKee et al. (2012) at age 24 years, and Gellerstedt and Aust (2004) at 15 years. Mean overstory biomass, lowerstory biomass, stem height, DBH, and overstory/lowerstory stem density were greatest in SKID (Tables 8, 9, 6, 4, 2 and 3, respectively).

Table 9

Average aboveground biomass of lowerstory species at 35 years. Letters indicate significant differences among treatments for a given species as indicated by a Wilcoxon Nonparametric Comparison test performed at $\alpha = 0.05$.

Treatment					
Species	HELI	SKID	GLYPH	REF	p-value
————— (Mg ha ⁻¹ ± standard error) —————					
<i>Acer rubrum</i>	0.9 (± 1.5)	2.2 (± 1.5)	2.4 (± 1.5)	–	0.7518
<i>Fraxinus caroliniana</i>	12.9 (± 2.4) a	8.2 (± 2.4) a	0.3 (± 2.4) b	1.5 (± 2.4) c	0.0018
<i>Nyssa aquatica</i>	0.1 (± 0.6) b	2.5 (± 0.6) a	0.2 (± 0.6) b	–	0.0110
<i>Taxodium distichum</i>	1.4 (± 0.9) ab	3.3 (± 0.9) a	0.02 (± 0.9) b	–	0.0453
All Species	20.6 (± 2.5) a	22.0 (± 2.5) a	4.9 (± 2.5) b	2.0 (± 2.5) b	< 0.0001

Table 10

Average of aboveground biomass. Letters indicate significant differences among treatments for a given stratum as indicated by a Tukey's HSD test performed at $\alpha = 0.05$.

Treatment	Overstory	Lowerstory	Ground flora	All strata
————— (Mg ha ⁻¹ ± standard error) —————				
p-value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
REF	515.6 (± 31.4) a	2 (± 2.5) b	0.12 (± 0.02) b	517.9 (± 31) a
SKID	317.2 (± 31.4) b	22 (± 2.5) a	0.03 (± 0.02) c	339.3 (± 31) b
HELI	272.8 (± 31.4) b	20.6 (± 2.5) a	0.04 (± 0.02) bc	293.5 (± 31) b
GLYPH	137 (± 31.4) c	4.9 (± 2.5) b	0.4 (± 0.02) a	142.3 (± 31) c

Conclusions

As with other long-term evaluations, previous findings need to be considered to provide context to the most recent analyses. A visual representation of changes across treatments during the previous 35 years is presented in Fig. 3. Prior to harvest treatment, the site was found to be generally uniform with regard to hydrology, soils, and vegetation, with water tupelo and baldcypress dominating the overstory with a smaller component of pumpkin and Carolina ash (Aust et al. 1990). In the two growing seasons following harvest, Aust and Lea (1991) predicted that the skidder treatment would have negative effects on subsequent stand growth due to the severe trafficking effects, which included increased soil mechanical resistance and decreased saturated hydraulic conductivity, soil oxygen, and soil redox potential. Conversely, Mader (1990) evaluated the net primary productivity and regenerating species on the site during the same periods and found that the HELI and SKID were both fully stocked, but black willow had become a significant proportion of the treatments. The discrepancies between the potentially negative soil disturbances and the somewhat altered species created some concerns that the area would have altered species and lower productivity.

Seven years after treatment installation, Aust et al. (1997) reevaluated the site and found that tree and stand aboveground volumes within the HELI and SKID were on track to be similar to anticipated levels as before harvest, but also found that the SKID volumes were actually greater than the HELI. The authors at this point attributed recovery of the HELI and SKID to increased evapotranspiration and associated lowering of water tables as well as the positive effects of sediment deposition from overbank flooding. At age 7 the GLYPH areas were herbaceous-dominated freshwater marshes, with extremely sparse black willow being the primary significant woody species.

Aust et al. (2006) evaluated the treatments again at age 16 years. At this age subtle differences were becoming apparent between HELI and SKID. Both treatments were adequately stocked with the same treatments as the REF, yet the HELI had a significantly higher pumpkin and Carolina ash component. SKID treatments had greater aboveground volumes and a higher water tupelo component. Aust et al. (2006) postulated that the differences in species between HELI and SKID was due to the initial disturbances that made SKID soils poorly aerated and favored the slightly more flood-tolerant water tupelo, while the ashes were favored within the less disturbed HELI. At age 16 years, black willow was a significant component within HELI and SKID. Meanwhile, GLYPH treatments were experiencing a gradual increase in woody species as woody seedlings slowly became established in the luxuriant herbaceous marsh conditions.

Twenty-four years after harvest, measurements of above- and belowground biomass (McKee et al. 2012) and overbank sediment accretion (Aust et al. 2013) were conducted. These measurements indicated that the black willow component was slightly smaller within SKID and HELI treatments and that the SKID disturbance had greater above- and belowground biomass. Interestingly, this evaluation also documented the greater belowground soil carbon component within SKID treatments, relative to HELI. Apparently, the initial skidder trafficking had buried a portion of woody material (slash, nonmerchantable material), which roots were preferentially exploiting for nutrients. Furthermore, sediment data revealed that rates of sediment accretion were stabilizing as canopies closed and the herbaceous vegetation was reduced by

lack of sunlight. Over the 24 years, all disturbance treatments accumulated more sediment than REF, with the GLYPH treatment accumulating the most due to the sediment trapping of the herbaceous component (Aust et al. 2012).

Consideration of the preceding measurements is needed to better interpret the 35-year results. Thirty-five years post-harvest, both SKID and HELI resulted in adequate stocking of species that are similar to the preharvest species as exemplified in REF. Both HELI and SKID are expected to retain species composition of the original stand. Interestingly, SKID, which was originally more disruptive to soils and internal water movement, seems to be recovering from the disturbance at a similar rate as HELI. As indicated by preceding evaluation, there are several potential explanations of this trend. First, the original species on the site were flood tolerant to very flood tolerant, thus they were capable of surviving in low oxygen status soils. Second, the wetter soil condition within SKID reduced the initial herbaceous competition and reduced the density of the slightly less flood-tolerant *Fraxinus* species within the site. Third, the microtopography created by rutting and soil displacement of SKID created areas of higher and potentially more aerated soils that favored preferential rooting of the regenerating species. Fourth, the species on the site have tremendous coppice regeneration capacities, which was evidenced by rapid growth from established root systems within both the HELI and SKID. Finally, annual deposition of sediments combined with shrink-swell soils have filled the ruts with noncompacted sediments. Cumulatively, these factors explain the positive recovery of HELI or SKID regeneration and growth for both tupelo and baldcypress.

The slow yet steady trend in recovery within GLYPH indicates the importance of both coppice and seed regeneration sources within similar forested wetlands, in the absence of advance reproduction. Trees that have established within GLYPH resulted from seed that floated in via floodwaters or was dispersed from nearby seed sources. These seed sources are of major importance to the recovery of herbaceous dominated wetlands that were formerly forested.

Finally, REF has lost biomass since the last remeasurement and indicates that the stand is transitioning from the late stem exclusion – early understory re-initiation stage of stand development. Overall, disturbances created by the SKID and HELI treatments are predicted to be of minimal effect to the ecosystem services provided by this forested wetland, and even the severe GLYPH treatment is anticipated to recover, albeit more slowly. These results indicate that the cumulative sources of resiliency from soil, hydrology, and vegetation features should be considered when evaluating the potential for ecosystem recovery following disturbance.

Abbreviations

REF

No harvest reference

HELI

Clearcutting with helicopter removal

SKID

Skidder extraction simulation

GLYPH

Broadcast spray (glyphosate) of sprouts and seedlings for two years

DBH

Diameter at breast height

BMP

Best management practice

MTRD

Mobile-Tensaw River Delta

Declarations

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Competing Interests

Drs. Aust, Coates, and Carter have received financial support for research from NCASI, and Dr. Schilling is employed by NCASI.

Author Contributions

WMA was an original investigator for the previous portions of the study. WMA, DRC, and TAC designed the 35-year remeasurement and remeasurement. WMA, DRC, and CE collected the data on the site. CE drafted the original manuscript as part of her Master of Forestry program, and WMA, DRC, and TAC served as her graduate committee. The original draft was by WMA, DRC, TAC, and EBS. EBS oversaw the financial assistance from NCASI. All authors have read and approved the manuscript.

Data Availability

The datasets from the current study are available from the corresponding author upon reasonable request.

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Figures

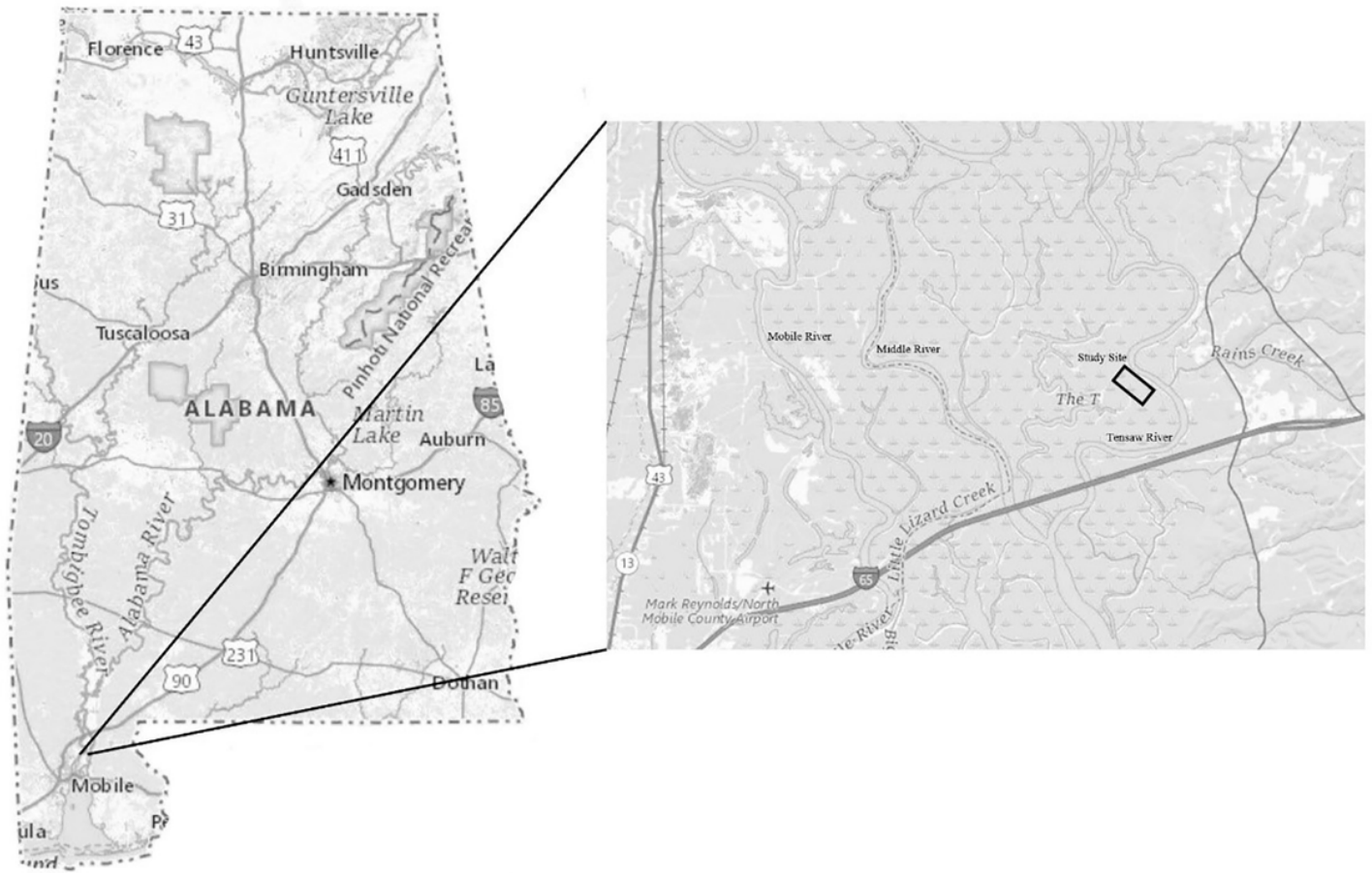


Figure 1

The Mobile-Tensaw River Delta (Tombigbee and Alabama River Basins) and approximate location of the study site. Adapted from USGS

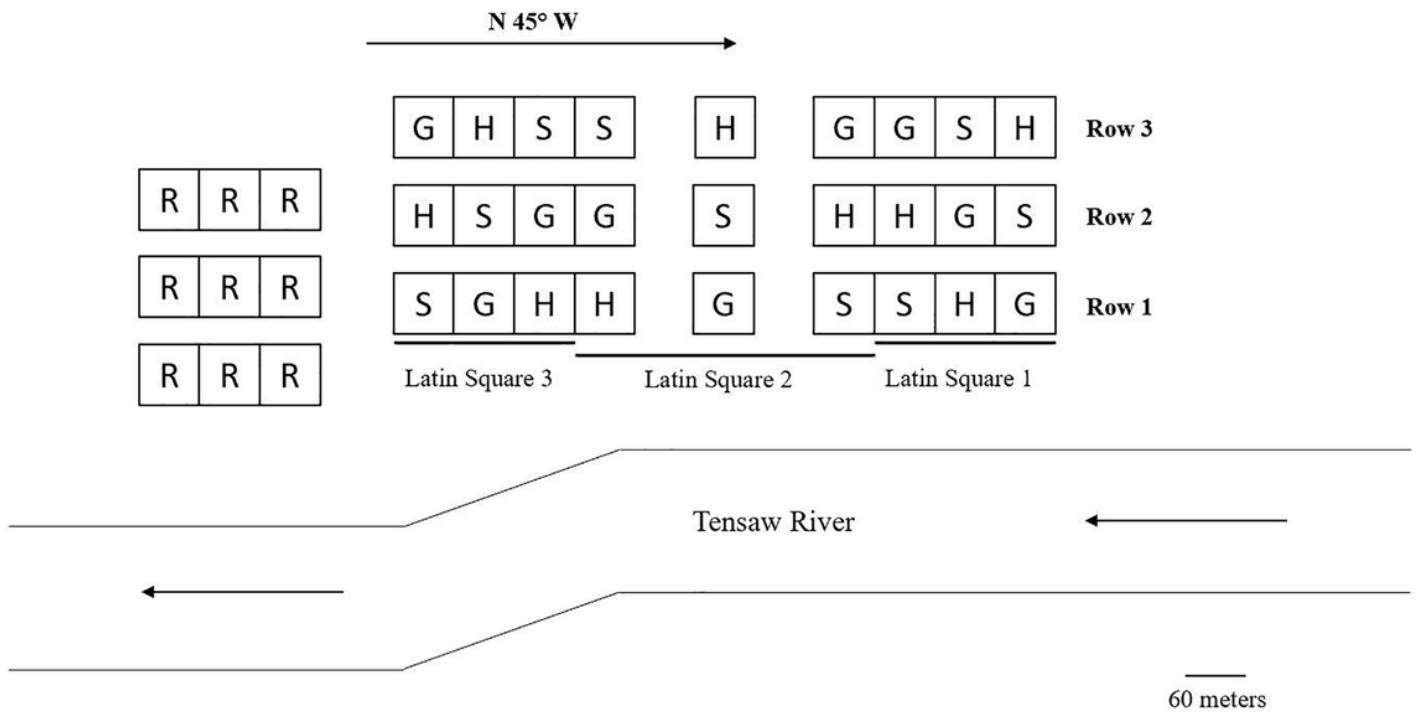


Figure 2

Study site treatment layout where each treatment cell measures 60 x 60m (86 ha). R = reference area (REF), S = skidder treatment (SKID), H = helicopter log removal (HELI), and G = glyphosate treatment (GLYPH). Adapted from Aust and Lea (1991)

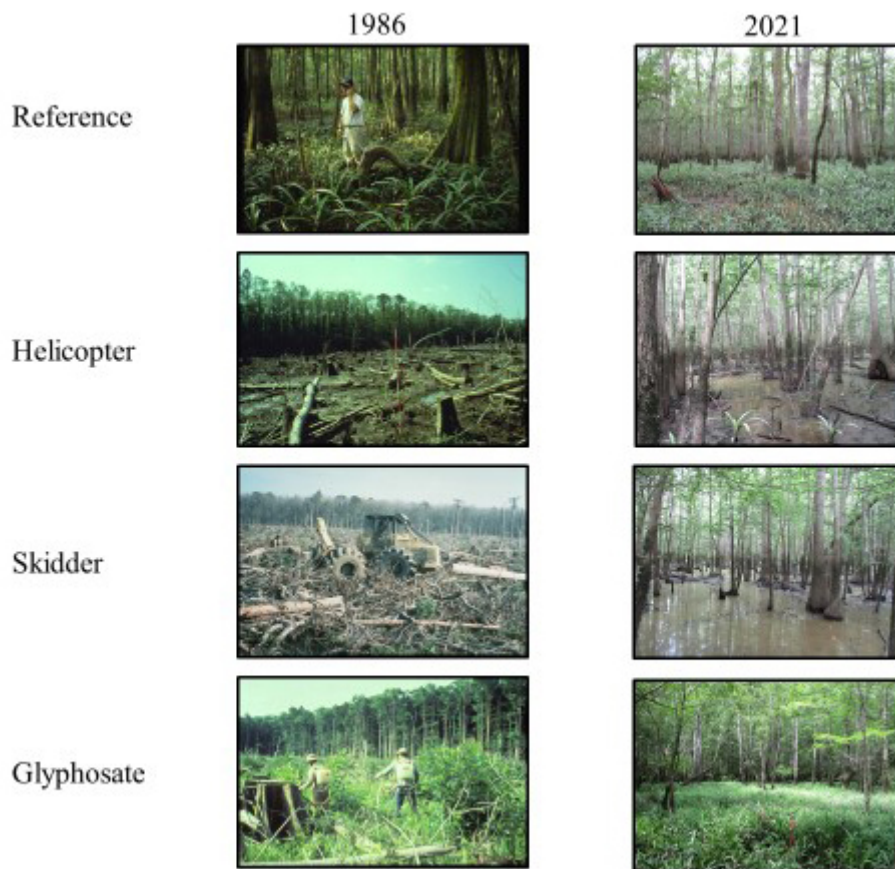


Figure 3

Visual comparison of the four disturbance levels in 1986 versus 2021 (35 years)