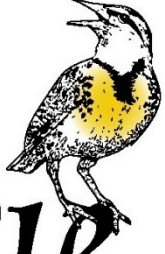


The Prairie Enthusiasts



Surface Water Investigation Report

Shea-Muller Wetland Sediment Removal and Restoration
River Planning Grant # RP35121

The Prairie Enthusiasts
Empire-Sauk Chapter
2845 Timber Lane
Verona, Wisconsin 53593

December 31, 2021



Introduction/Review:

The Prairie Enthusiasts (TPE) seeks continuation of the sediment removal and restoration project completed in 2012 on their Shea-Mueller site in Iowa County, WI. In partnership with Wisconsin Waterfowl Association, the US Fish and Wildlife Service, Cardno (now Stantec), and Jensen Ecology, TPE has created a plan for removal and restoration of eligible areas containing post-settlement silt on-property. Three of these areas were rented to a neighboring farmer as cropland until expiration lease agreement in December 2021. Another area included in the investigation is a fallow field recently acquired by TPE. As part of this surface water planning grant TPE investigated these fields to determine depth and quantity of post-settlement sediment layered above the native wetland soils. The investigation window was limited because the crops (corn) needed to be harvested prior to exploratory trenching and soil profiling. As part of this investigation the project team is submitting the following:

- Summary model of existing alluvium/post-settlement sediment on-site
- Plan for sediment removal and restoration
- Erosion control plan
- Seeding and live planting plan

Investigation

The team chose Tuesday, November 15th, 2021, as the investigation day, but predicted weather conditions were not observed in the field. The team was hoping for mostly sunny skies to better identify redox and leaching at different depths. Stratus clouds obscured the sun most the day, making it difficult to determine redox and leaching in native soils versus that within alluvium. Redox can occur in soil deposits if they are anoxic, so it's not uncommon to find redox in soil deposits that are 5+ years old (USDA, 2018).

The soil investigation involved trenching various portions of the fields to determine sediment depths. Trench locations were determined using data from preliminary core samples in 2018 and observations of stormwater flow on site over the past few years. The investigation fieldwork was supervised by Peter Ziegler (Wisconsin Waterfowl Association) who also oversaw the adjacent 2012 sediment removal and restoration project. Trenches higher in the landscape showed the B soil horizon near the surface and little to no oxidation in the A soil horizon. These areas were mapped as upland and may be used as temporary locations for spoil depending upon project timing. After the spoil is removed and grading is complete, these upland areas will be restored to mesic prairie.

Trenches lower in the landscape showed redox activity throughout, even 36-48 inches below the surface level. The sediment layer could be determined by looking at color differences during periods of sunlight, but light conditions were not favorable. Final depths were selected based on visible cues in the soil profiles and marked along the lengths of the trenches. The depths of the markers were recorded using a GPS unit calibrated to mean sea level (See attachment A: Photo Pages).

Sediment Modeling

The sediment estimate was derived by taking the average depths from the trenches and extrapolating it across the removal areas. The average sediment depth on the east side of the creek is approximately 30 inches while the fields on the west side came out to be 21 inches. Sediment depths in all fields ranged from less than 6 inches to deeper than 36 inches. The total acreage of all fields is approximately 9.6 acres, while the area of sediment removal is closer to 5.4 acres. The total estimated wetland gain from converted crop fields is 4.1 acres. Wetland enhancement in fallow areas is estimated at 1 acre. The total estimated yardage for removal is calculated at 10,000-12,000 square yards. By comparison, this is approximately 1/3 of the amount of sediment removed in 2012 (See Attachment B: Raw Data). This overall number may change based on variations in groundwater flow near the soil surface. These variations can best be identified during project implementation.

Removal Plan

The primary consideration of the design is to limit steep slopes and abrupt landscape variability across the site while maximizing establishment of high-quality native ecosystems. The current stormwater flow is mostly sheet flow slowed down by the restoration completed in 2012 although some occurrences of channelization are evident near the proposed fields of removal/restoration. The main objectives are to repair channelization, slow down stormwater flow from neighboring properties and promote a resilient suite of native vegetation to stabilize riparian areas. There are a few occurrences of groundwater near the soil surface as evidenced by aquatic emergent vegetation in areas restored in 2012. These areas are likely to expand with continued sediment removal and restoration, but we won't know the extent until project implementation is complete.

Removal of sediment would take place during the growing season, targeting a typical dry period of July-August. Removal would be a combination of excavator, dozer and haul truck or tractor scraper. Compaction will be minimized by using a tractor scraper, which has shown to be minimally impactful in similar projects. A dozer will be used along the edges to push sediment to upland areas and for grading within the removal areas and outside the removal areas. Removed sediment will be hauled off-site if possible.

There are areas restricted from soil disturbance surrounding the restoration zone. Some of the Shea-Mueller site is currently enrolled in the NRCS Conservation Reserve Program. Fortunately, many of these areas are already restored, and don't require additional disturbance. Near the South property line, several occurrences of *Carex tricornis* sod exist along the creek which outcompete reed canary grass and provide excellent stabilization of the streambank. The project team agrees that this native sod should remain undisturbed because it would be too difficult to re-establish in a timely manner. These issues factor in removal of sediment in the Eastern field: there aren't viable access routes to haul sediment from this portion of the site without violating NRCS regulations. The plan is to build out the existing slope using the spoil removed from the wetland. This portion of the field is out of the mapped floodplain.

All material has been identified to be moved to upland areas and out of the mapped floodplain around the exterior of the excavation sites. The entire west side would incorporate the Moundview rd. Right-Of-Way extending in the current field. Using the ROW increases the area for placement and helps to stabilize the road shoulder prolonging the life of the road. Additional material could be hauled off site by contractor if it is beneficial to the project. This will depend on the contractor, timing of removal and permitting. Initial conversations with nearby farmers indicate desire to haul and distribute any extra spoil to crop fields higher in the landscape. Much of the spoil is high in organic matter and nutrients which would likely improve places with shallow topsoil. Updated agricultural practices and regulations of the past few decades have greatly reduced sediment runoff (See Attachment C: Figures).

Erosion

Completion during the growing season would allow a sufficient cover crop to establish as quickly as possible post-construction. The entire area would be seeded with a cover crop appropriate for establishing native planting communities ranging from emergent marsh to wet prairie to mesic prairie. At a minimum NRCS Tech note 340 cover crop would provide the base guidelines we would follow. Based on project timing, TPE may allow the neighboring farmer to plant a forage crop to stabilize bare soil prior to removal. In addition, the bare soil areas would be mulched with certified weed seed free straw. Permanent cover will be planted at the appropriate timing to allow for best establishment. This is anticipated to be a mix of native wetland and prairie seed mixes comparable to the adjacent restoration area completed in 2012. This area will also act as a well-established buffer which along most of the site is greater than 100ft. The buffer becomes minimal at 30ft along one stretch on the east side and along the SE field. Both areas have concentrated surface outflows and will receive a rock grade control structure to stop and prevent further head cutting. On the surface above them straw wattles will be used to slow sheet flow and catch sediment during the vegetation establishment period. If the excess spoil needs to be stockpiled on-site due to project timing, the piles would be protected with straw mulch and silt fencing if necessary.

Restoration, Seeding and Live planting

Site restoration will take place after grading is complete and heavy equipment no longer needs to access the site. Upland areas not used for spoil storage will be planted with a mesic seed mix. Wetland areas will be planted with a wet seed mix with a transition between wet and mesic areas. Rates for seeding will be based on the goal of spreading 50-100 native seeds per square foot. Cover crop seeding rates will be 20-50 seeds per square foot. This strategy is sometimes successful if the goal is to establish a site in 1 year. TPE has had success with supplemental seeding paired with prescribed burning for multiple years to establish diverse plant communities. The strategy is that certain species are more productive certain years based on conditions. The site will be heavily seeded initially to establish native plants, however more conservative species will be added several years after the initial seeding. This strategy also provides opportunity to spot spray and re-seed occurrences of invasive species before they become established as well.

The plan includes installation of live plants and micro-topography enhancement to promote tussock formation on site. This will involve manual manipulation of the soil using hand tools to mimic conditions in climax sedge meadow. Aquatic emergent areas will be live planted to increase the speed of establishment and prevent loss of seed from runoff within aquatic emergent zones. Live plants and seed will be sourced within the driftless ecoregion. Seed for forbs will likely be purchased but may be collected from native seed sources nearby. The genotype of grasses is more widespread across large geographic regions, so local sources aren't as important. Native grass seed will be reasonably sourced from near the driftless ecoregion.

If native seed isn't available at the time of restoration, cover crops will be installed at a higher volume to stabilize the soil. Native seed will be distributed appropriately as soon as site conditions are favorable. Restoration of spoil areas will occur after stored spoil is removed from the site. The project team is optimistic there will be local demand for the nutrient-rich soil which may reduce the necessity of storing it on site for a long period of time.

Site maintenance is planned to take place several times throughout the year. TPE has 2 full time-staff, 4-5 seasonal interns, and numerous volunteers tasked with site survey, seed collection, prescribed burning, and invasive species management. All land management for Shea Muller and the rest of Mounds View Grasslands is coordinated by the site steward, Rich Henderson. Currently, non-crop areas of the Shea-Muller site are under management by staff and contractors funded through the Wildlife Habitat Partnership Fund grant. This work involves removal of non-native woody species, prescribed burning, and sweeping the site for invasive plants. Continual maintenance of these diverse native communities surrounding the project area help to stabilize the watershed of Williams-Barneveld creek (See Attachment C: Plan Figures)

Conclusion

The project team is confident in the plan to continue sediment removal and restoration in the watershed of Williams Barneveld creek. Project timing is dependent on weather which is why there is variability included in the plans. The other major factor is funding source and timing of award. The team is hopeful implementation of project will be eligible for continued funding from the Surface Water Grant Program. As TPE grows as an organization we are grateful to have so many professionals willing to assist with habitat improvement projects. We look forward to continued partnerships with the Wisconsin DNR in protection and enhancement of natural areas.

References:

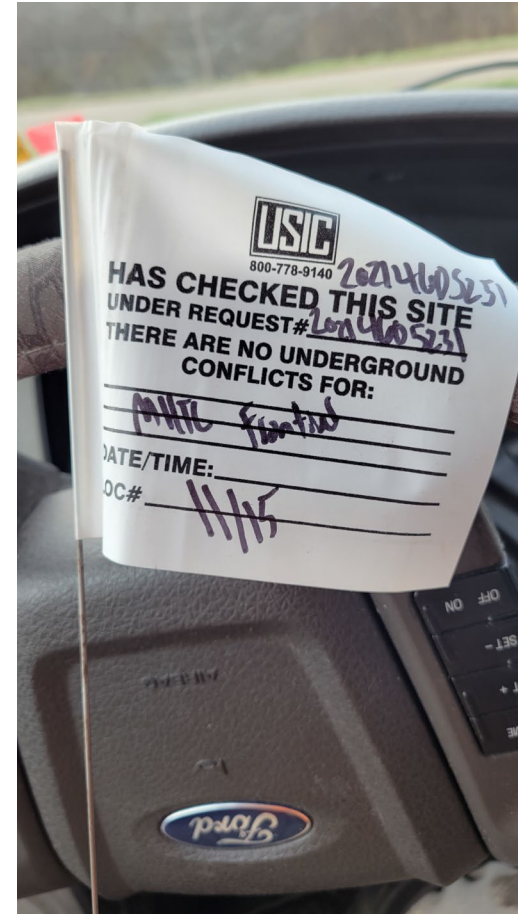
1. United States Department of Agriculture, NRCS: *Field indicators of Hydric Soils in the United States*, Version 8.2, 2018, Edited by L.M. Vasilas, Soil Scientist, NRCS, Washington, DC; G.W. Hurt, Soil Scientist, University of Florida, Gainesville, FL; and J.F. Berkowitz, Soil Scientist, USACE, Vicksburg, MS
2. Other sources include field experts on the project team:
 - Rich Henderson, TPE, Wisconsin DNR(Retired), Research Ecologist specializing in native ecosystem management
 - Pat Trochlell, TPE, Wisconsin DNR (Retired), Wetlands Biologist/Mitigation expert
 - Peter Ziegler, Wisconsin Waterfowl Association, Wetland Restoration expert
 - Mike Engel, USFWS, Private Lands Biologist/Ecology expert
 - Nicole Staskowski, Cardno(Stantec), Professional Wetland Scientist/Ecology expert
 - Jens Jensen, Jensen Ecology, Ecological Restoration expert
 - Andrew Sleger, TPE, Ecological Restoration specialist
 - Excavation:
 - Charlie with B&C Excavation, Barneveld, WI
 - Observers:
 - Tally Hamilton, Ducks Unlimited Biologist
 - Eric Grycan, The Prairie Enthusiasts, assistant land manager

Attachment A: Photo Pages

Shea-Mueller Site investigation: 11/9/21-11/15/21



The crops were harvested by 11/9/2021 making it possible for the project team to begin the investigation.



Digger's hotline was contacted, and the site was ready for trenching investigation on 11/15/21. The project team agreed to complete the investigation due to the gun deer season for safety reasons.



Shea-Mueller Site investigation: 11/15/21



The predicted weather was “mostly sunny” which would have been good for identification of soil profiles. The weather was mostly cloudy on the day of investigation making it difficult to visually determine sediment levels. Markers were placed in the trenches at appropriate depths (considering final landscape positioning) and recorded using a GPS unit calibrated to mean sea levels provided by USFWS.

Shea-Mueller Site investigation: 11/15/21



The walls of the excavated trenches were chipped away to clearly see the soil layers.



The project team found evidence of leaching into the inorganic B soil horizon in certain spots.

Shea-Mueller Site investigation: 11/15/21



A steep erosion cut exists along the creek near the fallow field at the south of the project area. This area will be addressed as part of the project.



Sediment depths on the East side of Williams Barneveld creek were deeper than those measured on the West side. The color of the profiles were also difficult to determine to extensive mixing of the layers.



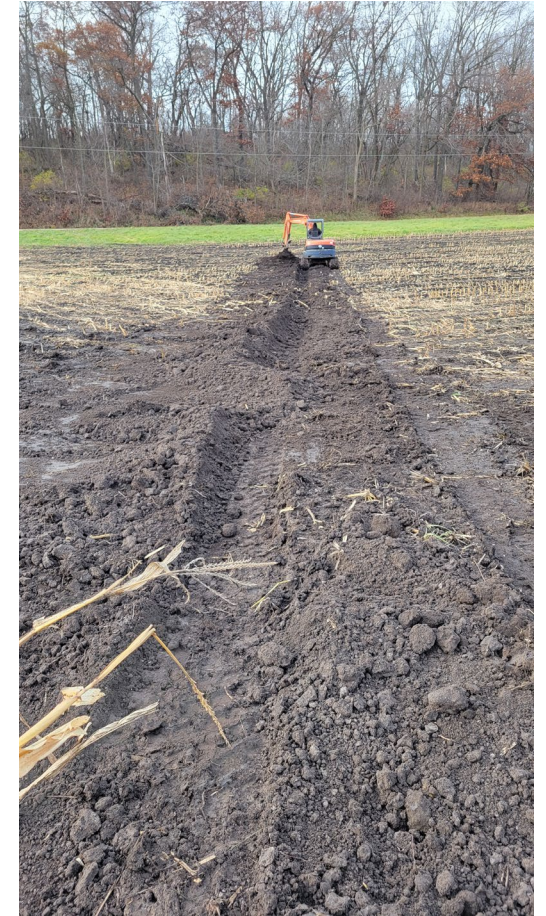
Shea-Mueller Site investigation: 11/15/21



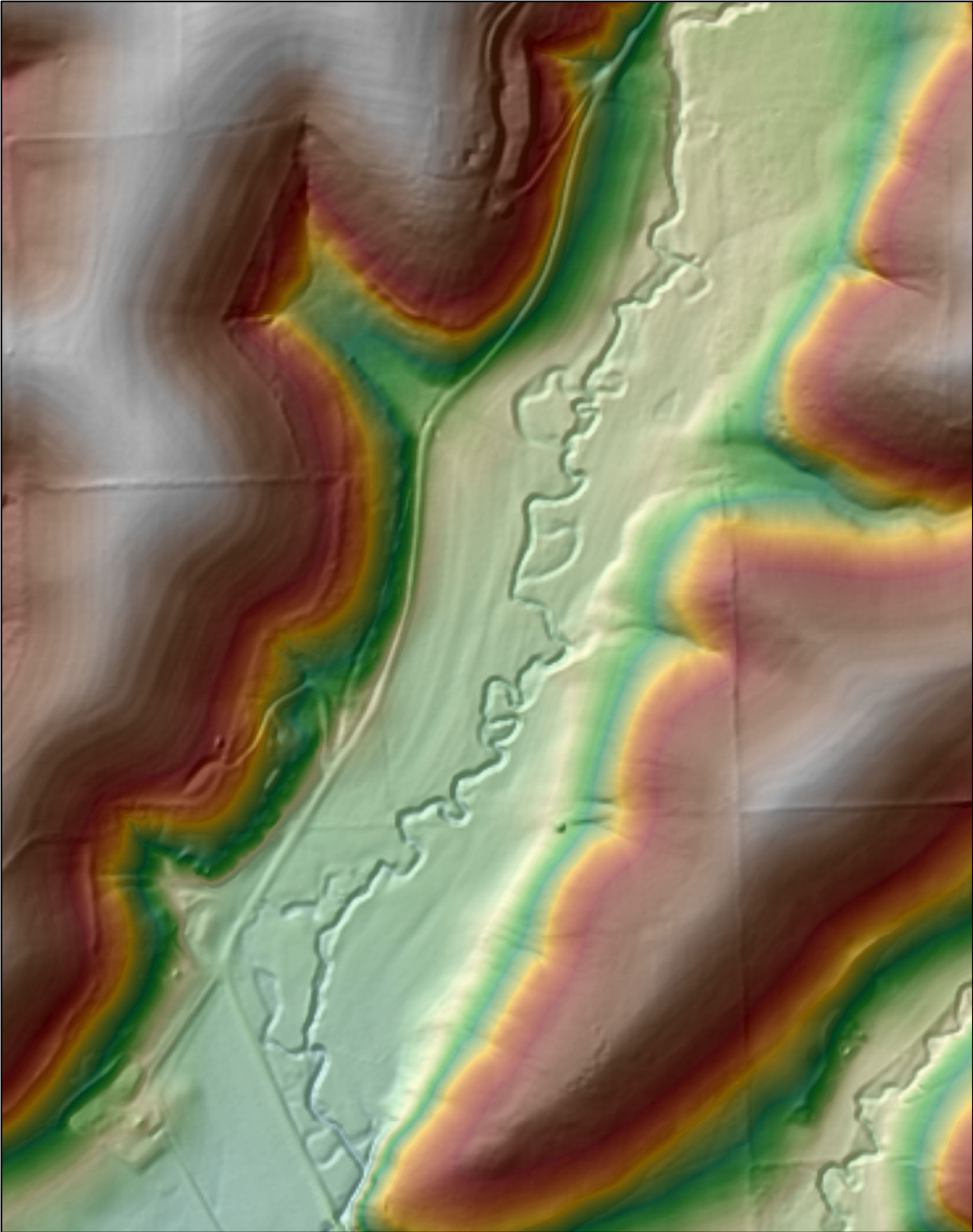
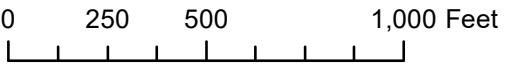
GPS points and elevations were recorded at known locations to act as benchmarks prior to project implementation.

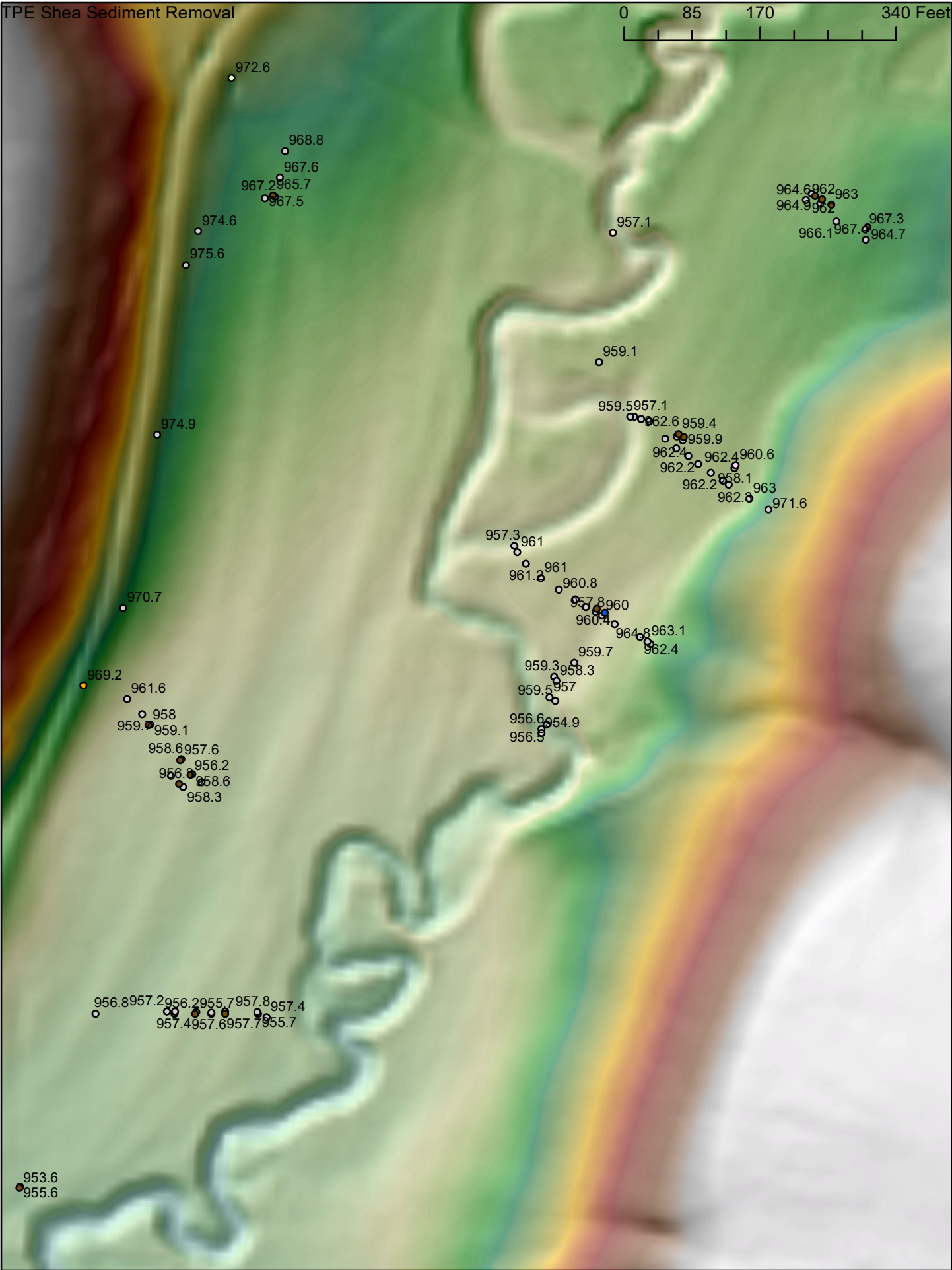


Exploration trenches were filled and graded prior to leaving the site. Note the middle photo: The native prairie in the uplands owned by TPE vs. the pine trees off-property and down stream. TPE hopes to acquire this neighboring property and continue the restoration of the watershed in the future.



Attachment B: Raw Data





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Polygon



Watershed
Delineation

Measure

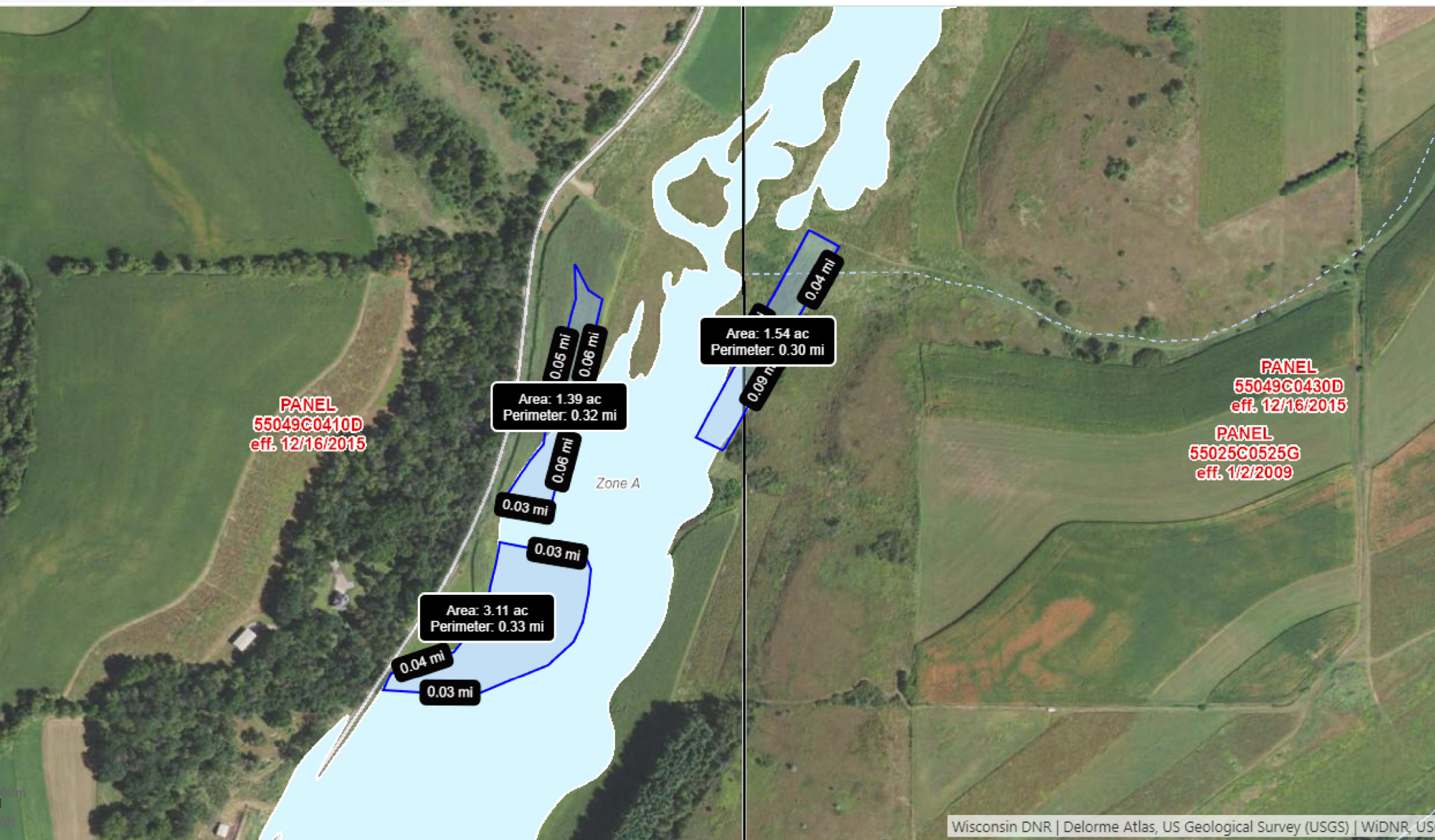


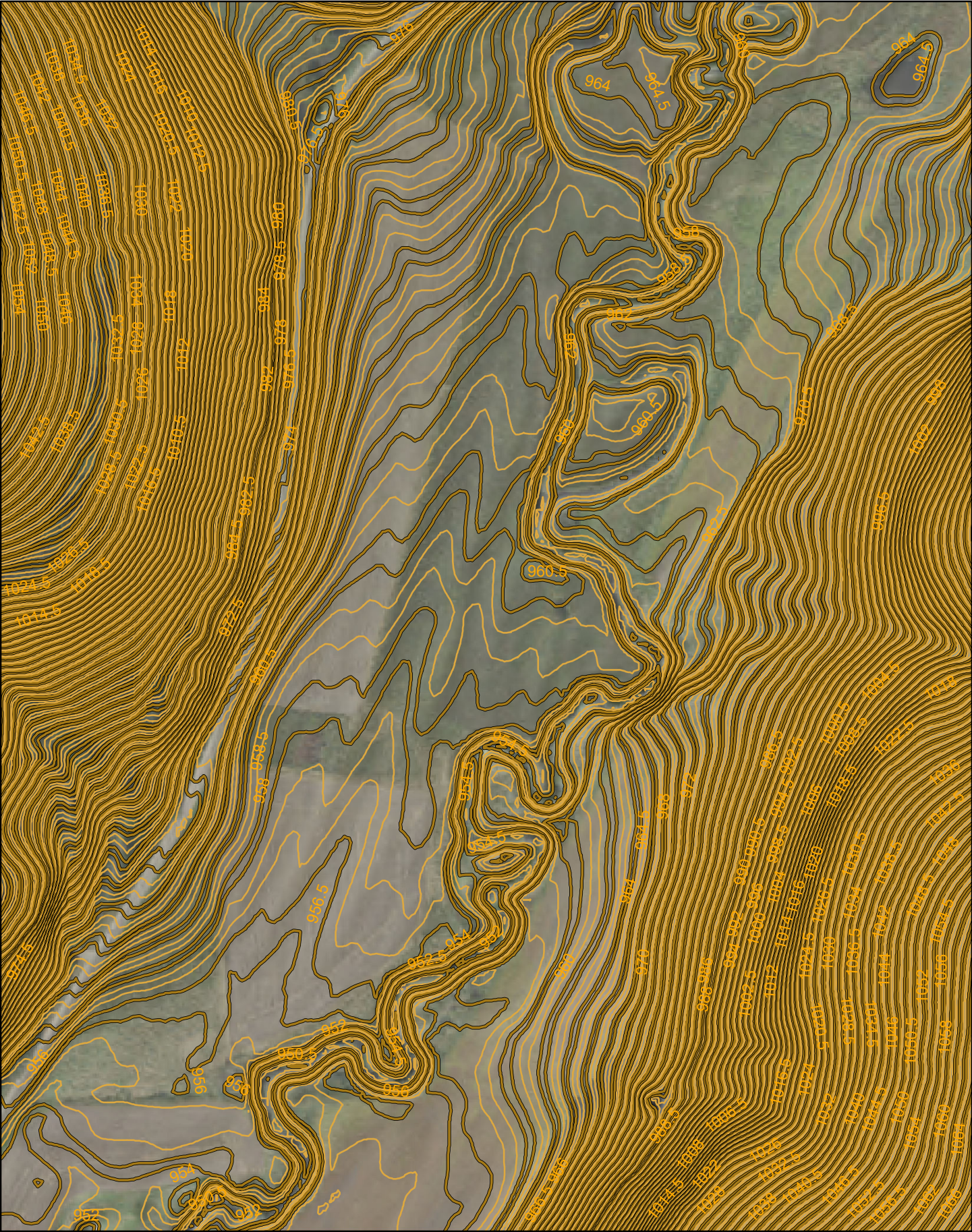
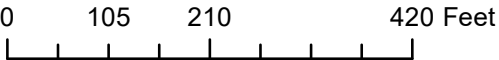
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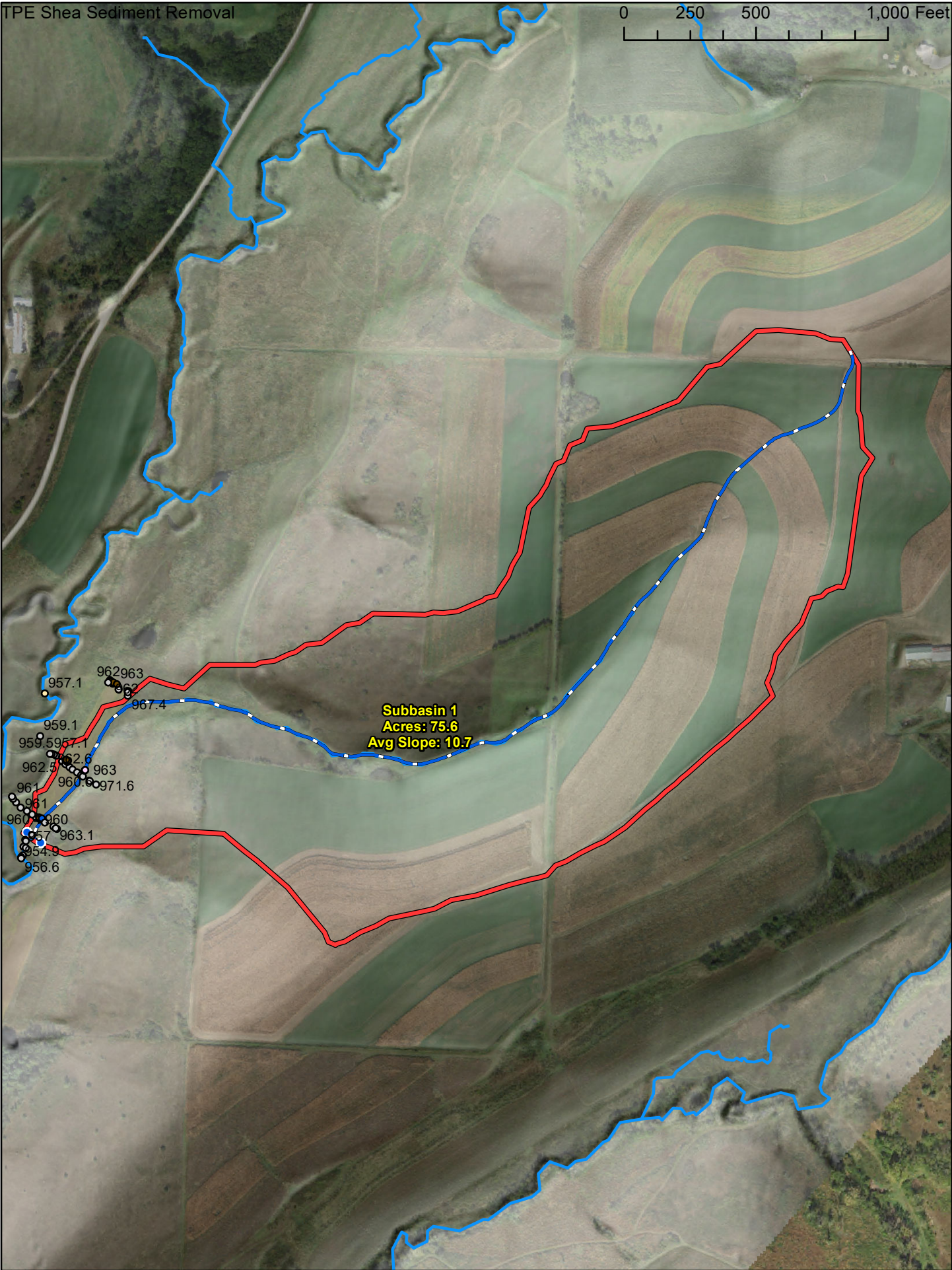
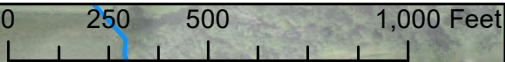


Export Drawings

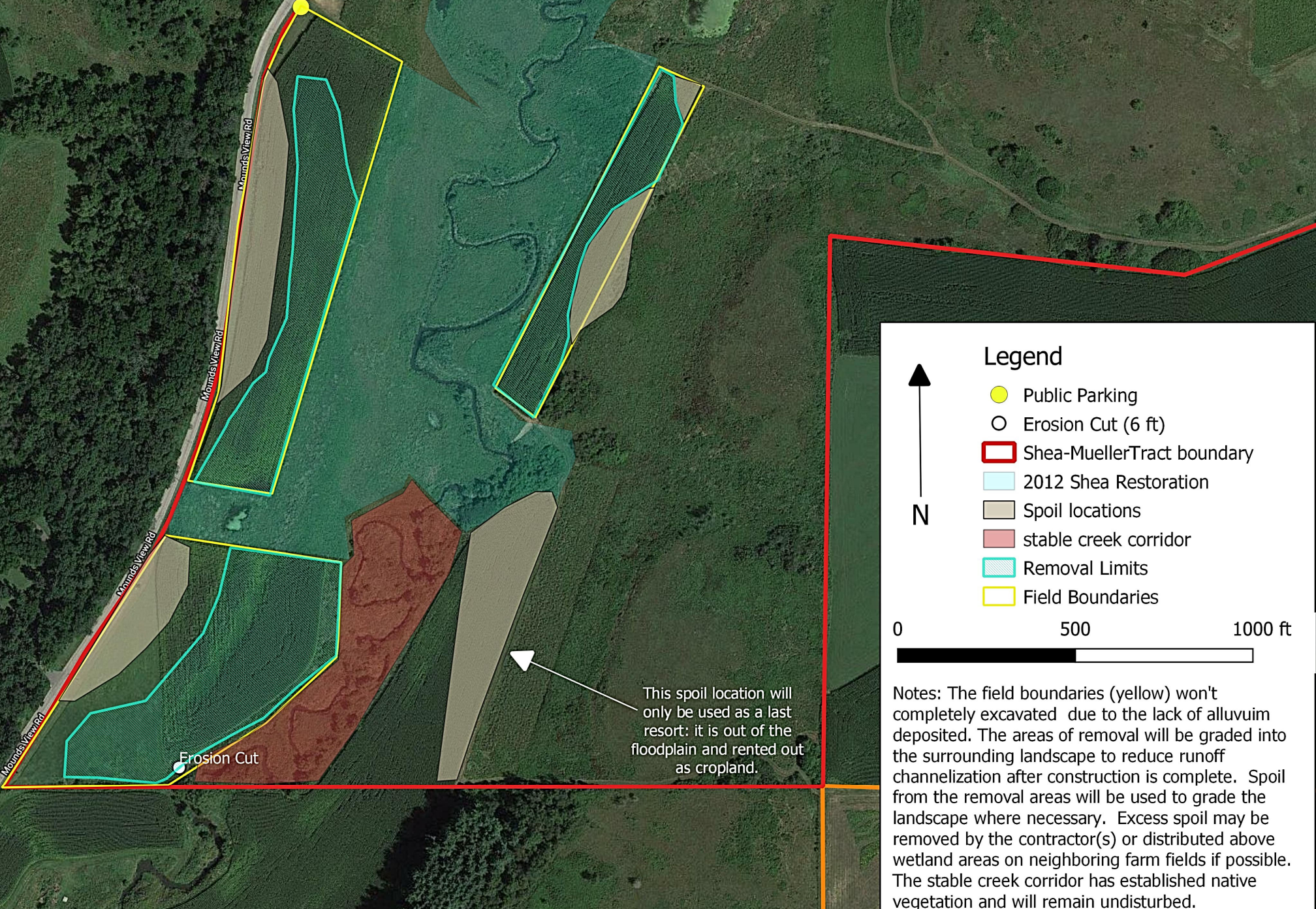
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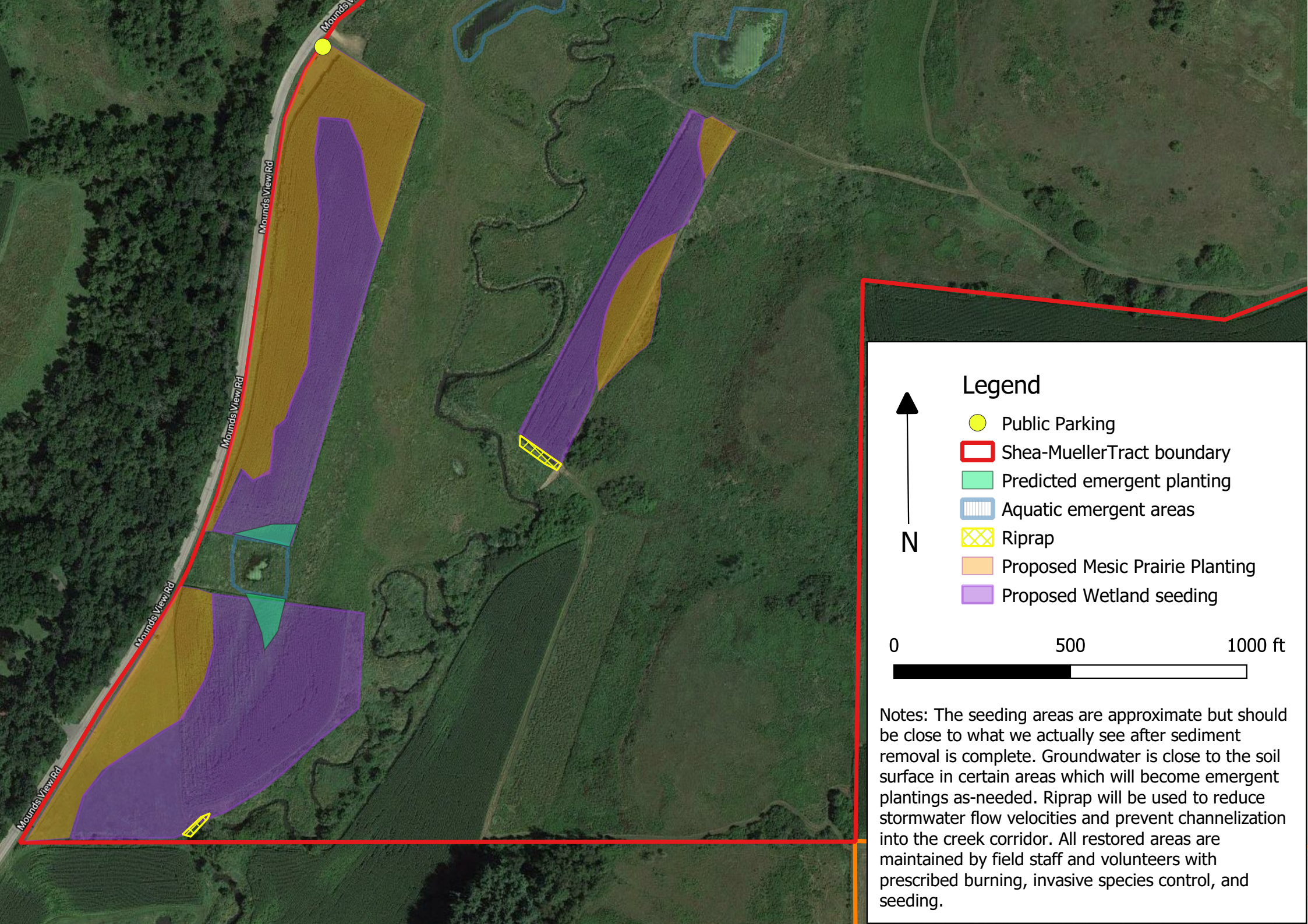






Attachment C: Plan Figures





Legend



- Public Parking
- Shea-Mueller Tract boundary
- Predicted emergent planting
- Aquatic emergent areas
- Riprap
- Proposed Mesic Prairie Planting
- Proposed Wetland seeding

0 500 1000 ft

Notes: The seeding areas are approximate but should be close to what we actually see after sediment removal is complete. Groundwater is close to the soil surface in certain areas which will become emergent plantings as-needed. Riprap will be used to reduce stormwater flow velocities and prevent channelization into the creek corridor. All restored areas are maintained by field staff and volunteers with prescribed burning, invasive species control, and seeding.

Attachment D: Seed Mixes



SITE NAME:	Mounds View Grassland		PLANT COMMUNITY:	Southern Sedge Meadow
ASSESSMENT AREA NAME:	Shea Wetland Restoration Site		SURVEYORS:	
GPS COORDINATES (Decimal Degrees)	Latitude:		SURVEY DATE:	
	Longitude:			
COUNTY:	Iowa		SITE NOTES:	List of possible species for southern sedge meadow restoration
ECOREGION (LEVEL III):	Driftless Area			

RESULTS:		Non-Natives			Floristic Quality Metrics: Native Species (n)				Floristic Quality Metrics: All Species (a)				wC _a By Growth Form:			
N _a	N _n	N _{int.}	Non-Native Total Cover:	Non-Native Relative Cover	FQI _n	w FQI _n	Mean C _n	Weighted Mean C wC _n	FQI _a	w FQI _a	Mean C _a	Weighted Mean C wC _a	Tree	Shrub	Herb	Aquatic
58	58	0	0%	0%	39.4	40.6	5.2	5.3	39.4	#VALUE!	5.2	#VALUE!	0.0	#DIV/0!	5.3	#DIV/0!
													0%	0%	60%	0%
													:Total Cover			

ENTER SPECIES CODE:	ENTER % COVER:	Scientific Name	Common Name	C-Value	Wetland Ind. Status (MW/NCNE)	WI Status	Growth Form	Duration	NHI Status	Invasive (NR40) Status	Accepted ITIS Name
carstr	20	<i>Carex stricta</i>	tussock sedge	7	OBL	Native	herb	perennial	0	0	<i>Carex stricta</i>
eutmac	30	<i>Eutrochium maculatum</i>	spotted Joe-Pye-weed	4	OBL	Native	herb	perennial	0	0	<i>Eutrochium maculatum</i>
carlac	10	<i>Carex lacustris</i>	common lake sedge	6	OBL	Native	herb	perennial	0	0	<i>Carex lacustris</i>
thadas		<i>Thalictrum dasycarpum</i>	purple meadow-rue, tall meadow-rue	4	FACW	Native	herb	perennial	0	0	<i>Thalictrum dasycarpum</i>
rumbri		<i>Rumex britannica</i>	greater water dock, British dock	8	OBL	Native	herb	perennial	0	0	<i>Rumex britannica</i>
onoson		<i>Onoclea sensibilis</i>	sensitive fern	5	FACW	Native	herb	perennial	0	0	<i>Onoclea sensibilis</i>
calcan		<i>Calamagrostis canadensis</i>	blue-joint grass	5	OBL	Native	herb	perennial	0	0	<i>Calamagrostis canadensis</i>
epilep		<i>Epilobium leptophyllum</i>	American marsh willow-herb, bog willow	8	OBL	Native	herb	perennial	0	0	<i>Epilobium leptophyllum</i>
ascinc		<i>Asclepias incarnata</i>	swamp milkweed	5	OBL	Native	herb	perennial	0	0	<i>Asclepias incarnata</i>
cicbul		<i>Cicuta bulbifera</i>	bulblet water-hemlock	7	OBL	Native	herb	perennial	0	0	<i>Cicuta bulbifera</i>
scugal		<i>Scutellaria galericulata</i>	common skullcap, marsh skullcap	5	OBL	Native	herb	perennial	0	0	<i>Scutellaria galericulata</i>
lycuni		<i>Lycopus uniflorus</i>	northern bugleweed, northern water-hc	4	OBL	Native	herb	perennial	0	0	<i>Lycopus uniflorus</i>
galtrifi		<i>Galium trifidum</i>	northern three-lobed bedstraw, small b	6	FACW	Native	herb	perennial	0	0	<i>Galium trifidum</i>
camapa		<i>Campanula aparinoides</i>	marsh bellflower	7	OBL	Native	herb	perennial	0	0	<i>Campanula aparinoides</i>
saglat		<i>Sagittaria latifolia</i>	broad-leaved arrowhead	3	OBL	Native	aquatic	perennial	0	0	<i>Sagittaria latifolia</i>
spaeur		<i>Sparganium eurycarpum</i>	broad-fruit bur-reed, common bur-reed,	5	OBL	Native	aquatic	perennial	0	0	<i>Sparganium eurycarpum</i>
carsco		<i>Carex scoparia</i>	broom sedge, lance-fruited oval sedge	4	FACW	Native	herb	perennial	0	0	<i>Carex scoparia</i>



ENTER SPECIES CODE:	ENTER % COVER:	Scientific Name	Common Name	C-Value	Wetland Ind. Status (MW/NCNE)	WI Status	Growth Form	Duration	NHI Status	Invasive (NR40) Status	Accepted ITIS Name
lysthy		<i>Lysimachia thyrsiflora</i>	swamp loosestrife, tufted loosestrife	7	OBL	Native	herb	perennial	0	0	<i>Lysimachia thyrsiflora</i>
mencan		<i>Mentha canadensis</i>	field mint, wild mint	3	FACW	Native	herb	perennial	0	0	<i>Mentha arvensis</i>
spialb		<i>Spiraea alba</i>	white meadowsweet	4	FACW	Native	shrub	perennial	0	0	<i>Spiraea alba</i>
carpel		<i>Carex pellita</i>	broad-leaved woolly sedge	4	OBL	Native	herb	perennial	0	0	<i>Carex pellita</i>
persag		<i>Persicaria sagittata</i>	arrow-leaved tearthumb, arrow vine	6	OBL	Native	herb	annual	0	0	<i>Persicaria sagittata</i>
latpal		<i>Lathyrus palustris</i>	marsh pea, marsh vetchling, slender-ste	5	FACW	Native	herb	perennial	0	0	<i>Lathyrus palustris</i>
eupper		<i>Eupatorium perfoliatum</i>	boneset, common boneset, thoroughw	6	OBL/FACW	Native	herb	perennial	0	0	<i>Eupatorium perfoliatum</i>
scicyp		<i>Scirpus cyperinus</i>	wool-grass	4	OBL	Native	herb	perennial	0	0	<i>Scirpus cyperinus</i>
spapec		<i>Spartina pectinata</i>	prairie cord grass, slough grass	5	FACW	Native	herb	perennial	0	0	<i>Spartina pectinata</i>
symfir		<i>Symphotrichum firmum</i>	glossy-leaved aster	6	OBL	Native	herb	perennial	0	0	<i>Symphotrichum firmum</i>
irivir		<i>Iris virginica</i>	southern blue flag, Virginia iris	5	OBL	Native	herb	perennial	0	0	<i>Iris virginica</i>
carutr		<i>Carex utriculata</i>	common yellow lake sedge, Northwest	7	OBL	Native	herb	perennial	0	0	<i>Carex utriculata</i>
pycvir		<i>Pycnanthemum virginianum</i>	common mountain mint, Virginia moun	6	FACW	Native	herb	perennial	0	0	<i>Pycnanthemum virginianum</i>
helaut		<i>Helenium autumnale</i>	common sneezeweed	4	FACW	Native	herb	perennial	0	0	<i>Helenium autumnale</i>
carbeb		<i>Carex bebbii</i>	Bebb's oval sedge, Bebb's sedge	4	OBL	Native	herb	perennial	0	0	<i>Carex bebbii</i>
verhas		<i>Verbena hastata</i>	blue vervain, simpler's-joy, swamp verb	3	FACW	Native	herb	biennial/per	0	0	<i>Verbena hastata</i>
sciatr		<i>Scirpus atrovirens</i>	black bulrush, dark-green bulrush	3	OBL	Native	herb	perennial	0	0	<i>Scirpus atrovirens</i>
bidtri		<i>Bidens tripartita</i>	straw-stem beggar-ticks, swamp marig	5	OBL/FACW	Native	herb	annual	0	0	<i>Bidens tripartita</i>
peramp		<i>Persicaria amphibia</i>	water heart's-ease, water smartweed	5	OBL	Native	herb	perennial	0	0	<i>Persicaria amphibia</i>
caltpal		<i>Caltha palustris</i>	cowslip, marsh-marigold, yellow marsh	6	OBL	Native	herb	perennial	0	0	<i>Caltha palustris</i>
lycame		<i>Lycopus americanus</i>	American water-horehound, common w	4	OBL	Native	herb	perennial	0	0	<i>Lycopus americanus</i>
cicmac		<i>Cicuta maculata</i>	common water-hemlock, spotted water	6	OBL	Native	herb	perennial	0	0	<i>Cicuta maculata</i>
mimrin		<i>Mimulus ringens</i>	Allegheny monkey-flower, monkey-flow	6	OBL	Native	herb	perennial	0	0	<i>Mimulus ringens</i>
angatr		<i>Angelica atropurpurea</i>	common great angelica, great angelica,	6	OBL	Native	herb	perennial	0	0	<i>Angelica atropurpurea</i>
poapal		<i>Poa palustris</i>	fowl meadow grass, marsh bluegrass	5	FACW	Native	herb	perennial	0	0	<i>Poa palustris</i>
cheglab		<i>Chelone glabra</i>	turtlehead, white turtlehead	7	OBL	Native	herb	perennial	0	0	<i>Chelone glabra</i>
symlan		<i>Symphotrichum lanceolatum</i>	panicked aster	4	FAC/FACW	Native	herb	perennial	0	0	<i>Symphotrichum lanceolatum</i>
galasp		<i>Galium asprellum</i>	rough bedstraw	7	OBL	Native	herb	perennial	0	0	<i>Galium asprellum</i>
epicil		<i>Epilobium ciliatum</i>	American willow-herb, hairy willow-her	3	FACW	Native	herb	perennial	0	0	<i>Epilobium ciliatum</i>
pilpum		<i>Pilea pumila</i>	Canadian clearweed	3	FACW	Native	herb	annual	0	0	<i>Pilea pumila</i>
stelon		<i>Stellaria longifolia</i>	long-leaved stitchwort	5	FACW	Native	herb	perennial	0	0	<i>Stellaria longifolia</i>
acoame		<i>Acorus americanus</i>	sweet-flag	7	OBL	Native	herb	perennial	0	0	<i>Acorus americanus</i>

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Seed mixes for Shea Mesic, Wet mesic, Wet areas.						
Species quantities for the final installation are based upon what is available						
			Dry Mesic	Mesic	Wet mesic	wet
	Amorpha canescens	Lead-plant	38	22	2	x (5)
	Andropogon gerardi	Big bluestem	52	35	32	x (73)
	Anemone canadensis	Meadow anemone		12	35	x (32)
	Anemone cylindrica	Thimbleweed	6	16	10	
	Angelica atropurpurea	Great angelica			p (4)	x (23)
	Antennaria spp	Pussytoes	14	9	8	x (14)
	Asclepias incarnata	Swamp milkweed			5	x (32)
	Astragalus canadensis	Canadian milkvetch		3	1	
	Baptisia lactea (alba)	White wild indigo	3	10	5	x (9)
	Baptisia bracteata	Cream wild indigo	5	5	5	
	Bouteloua curtipendula	Side oats grama	50			
	Calamagrostis canadensis	Bluejoint grass		15	17	x (91)
	Caltha palustris	Marsh marigold				x (32)
	Campanula aparinoides	Marsh bell-flower			p (4)	x (18)
NP	Chelone glabra	Turtlehead				x (18)
	Cicuta maculata	Water-hemlock			5	x (18)
	Cirsium discolor	Pasture thistle	2	12	12	x (27)
	Comandra umbellata	False toadflax	17	24	34	x (36)
	Coreopsis palmata	Prairie tickseed	30	26	2	x (9)
	Desmodium canadense	Showy tick-trefoil	1	5	12	x (46)
	Desmodium illinoense	Illinois tick-trefoil	8	22	5	
	Dodecatheon meadia	Shooting star	15	25	20	x (41)
NP	Echinacea pallida	Pale purple coneflow	45	26		
	Elymus riparius	Riverbank rye				x (?)
	Elymus virginicus	Virginia wild rye			1	x (?)
	Eriophorum angustifolium	Cotton-grass				x (23)
NP	Eryngium yuccifolium	Rattlesnake master	11	14	11	x (9)
	Eupatorium altissimum	Upland bonset		2		
	Eupatorium maculatum	Spotted joe-pye weed			12	x (41)
	Eupatorium perfoliatum	Common boneset			19	x (27)
	Euphorbia corollata	Flowering spurge	45	47	7	x (23)

NP	Euthamia graminifolia	Grass-leaved goldenrod		12	16	x (23)
	Fragaria virginiana	Wild strawberry	4	30	37	x (77)
	Galium tinctorium	Stiff bedstraw		10	10	x (23)
NP	Gaura biennis	Biennial gaura	1	2	2	
NP	Gentiana alba	Cream gentian		1	2	
	Gentiana andrewsii	Bottle gentian		11	7	x (36)
	Gentianella quinquefolia	Stiff gentian	13	5		
NP	Gentianopsis crinita	Fringed gentian			p (6)	x (9)
	Geum canadense	White avens				x (5)
	Geum triflorum	Prairie smoke	17	1	6	
	Glyceria striata	Fowl meadow-grass			1	x (32)
NP	Hasteola suaveolens	Sweet Indian plantain				x (5)
	Helenium autumnale	Sneezeweed			32	x (14)
	Helianthus laetiflorus rigid	Prairie sunflower	40	34	1	
	Heliopsis helianthoides	False sunflower		12	6	x (23)
	Heuchera richardsonii	Prairie alum-root	5	10	19	x (41)
	Hieracium canadense fasc	Canada hawkweed		1	2	
NP	Hierochloe odorata	Sweet grass			1	x (23)
NP	Houstonia caerulea	Bluets				x (5)
	Hypoxis hirsuta	Yellow star-grass	5	30	35	x (55)
NP	Iris virginica shrevei	Blue flag			10	x (55)
	Lathyrus palustris	Marsh vetchling			16	x (55)
NP	Lathyrus venosus	Veiny pea	1	29	17	x (18)
	Lespedeza capitata	Round-headed bush	6	17	5	
NP	Liatris pycnostachya	Prairie blazing star		1	28	x (32)
NP	Lilium michiganense	Turk's cap lily		5	7	x (50)
NP	Lilium philadelphicum and	Prairie lily	35	20	p (7)	x (9)
	Lithospermum canescens	Hoary puccoon	9	7	12	x (9)
	Lobelia siphilitica	Great blue lobelia				x (14)
	Lobelia spicata	Pale spiked lobelia	8	3	3	x (32)
	Lycopus americanus	Common water-horehound			17	x (36)
	Lycopus uniflorus	Northern water-horehound				x (9)
	Lysimachia ciliata	Fringed loosestrife		1	2	x (9)
	Lysimachia lanceolata	Lance-leaved loosestrife		1	3	
	Lysimachia quadriflora	Narrow-leaved loosestrife		1	15	x (18)

	Lythrum alatum	Winged loosestrife			7	x (18)
	Monarda fistulosa	Wild bergamot	6	25	24	x (50)
NP	Napaea dioica	glade mallow			p (4)	x (4)
	Oenothera biennis	Common evening-pr	3	3	9	
	Onoclea sensibilis	Sensitive fern				x (32)
	Oxalis violacea	Violet wood-sorrel	18	14	p (4)	x (14)
	Oxypolis rigidior	Cowbane			5	x (73)
	Panicum leibergii	Prairie panic-grass	17	32	15	x (9)
	Panicum oligosanthos	Few-flowered panic	14	19	10	x (5)
	Panicum virgatum	Switch grass	2	6	20	x (4)
NP	Parnassia glauca	Fen grass-of-Parnassus			p (6)	x (23)
	Parthenium integrifolium	Wild quinine	7	11		
	Pedicularis canadensis	Wood betony	20	35	55	x (14)
	Pedicularis lanceolata	Swamp betony			15	x (32)
	Petalostemum candidum	White prairie clover	20	15		
	Petalostemum purpureum	Purple prairie clover	28	14	11	
	Phlox pilosa	Prairie phlox	17	30	32	x (59)
	Physalis heterophylla	Clammy ground-che	15	5	5	
	Physalis virginiana	Lance-leaved ground	16	12	4	
NP	Platanthera flava	Tubercled orchid			p (2)	x (4)
	Polemonium reptans	Jacob's ladder			3	x (23)
	Polygala sanguinea	Field milkwort	5		2	
	Polygala senega	Seneca snakeroot	12	15	35	x (18)
	Polygonum amphibium	Water knotweed			7	x (14)
	Potentilla arguta	Prairie cinquefoil	12	11	6	
	Potentilla simplex	Common cinquefoil		11	15	x (9)
	Pycnanthemum virginianu	Common mountain	2	5	15	x (82)
	Ranunculus hispidus	Marsh buttercup				x (5)
	Ranunculus rhomboideus	Prairie buttercup	2			
	Ratibida pinnata	Yellow coneflower	22	42	60	x (36)
	Rosa spp	Wild rose	13	53	34	x (35)
	Rudbeckia hirta	Black-eyed Susan	3	7	22	x (64)
	Rudbeckia laciniata	Wild golden-glow			2	x (4)
	Saxifraga pensylvanica	Swamp saxifrage			2	x (50)
	Schizachyrium scoparium	Little bluestem	66	21	34	

	<i>Silphium integrifolium</i>	Rosinweed	5	17	17	x (18)
	<i>Silphium laciniatum</i>	Compass plant	19	22	37	x (5)
	<i>Silphium perfoliatum</i>	Cup plant			3	x (5)
	<i>Sisyrinchium campestre</i>	Prairie blue-eyed grass	35	20	12	x (23)
	<i>Solidago missouriensis</i>	Missouri goldenrod	7	15	9	
	<i>Solidago nemoralis</i>	Old-field goldenrod	31	7	21	
	<i>Solidago rigida</i>	Stiff goldenrod	18	45	50	x (32)
	<i>Solidago speciosa</i>	Showy goldenrod	4	14	1	
	<i>Sorghastrum nutans</i>	Indian grass	10	18	10	x (18)
NP	<i>Spartina pectinata</i>	Prairie cord grass		7	13	x (96)
	<i>Sporobolus heterolepis</i>	Prairie dropseed	28	21	23	x (5)
	<i>Stachys palustris</i>	Marsh hedge-nettle			21	x (23)
	<i>Symphotrichum oolentang</i>	Sky-blue aster	18	17	30	x (14)
	<i>Symphotrichum ericoides</i>	Heath aster	26	46	22	x (5)
	<i>Symphotrichum firmus</i>	Shining aster			p (7)	x (27)
	<i>Symphotrichum laevis</i>	Smooth blue aster	16	52	40	x (5)
	<i>Symphotrichum lanceolatum</i>	Lance-leaved panicled aster			p (17)	x (55)
	<i>Symphotrichum novae-angliae</i>	New England aster		1	3	x (68)
	<i>Symphotrichum sericeus</i>	Silky aster	35	2		
	<i>Taenidia integerrima</i>	Yellow pimpernel		10	12	
	<i>Thalictrum dasycarpum</i>	Purple meadow-rue		12	21	x (86)
	<i>Thelypteris palustris</i>	Marsh fern			p (4)	x (55)
	<i>Tradescantia ohimensis</i>	Common spiderwort	49	44	54	x (41)
NP	<i>Vernonia fasciculata</i>	Common ironweed			9	
NP	<i>Veronicastrum virginicum</i>	Culver's root		8	19	x (77)
	<i>Vicia americana</i>	American vetch	1	16	25	x (18)
NP	<i>Viola cucullata</i>	Hooded violet		21	36	x (55)
	<i>Viola pedatifida</i>	Prairie violet	65	50	9	
	<i>Viola sororia</i>	Hairy wood violet		3	10	x
	<i>Zizia aurea</i>	Golden Alexander	14	18	60	x (73)

Planting Recommendations for MV wetland and low prairie areas											
Sedges (Carex)											
Originally Present	Priority	Species	Common Name	Full Sun	Part Shade	High pH	Standing Water	Sedge Meadow	Fen/Seep	Wet Prairie	Wet-Mesic Prairie
	L	alopecoidea	Foxtail sedge	x	x	x		x		x	
Yes	M	annectans	Yellow fox sedge	x				x		x	x
	H	aquaticus	Water sedge	x			x	x			
	H	atherodes	Slough sedge	x			x	x			
Yes	H	bebbii	Bebb's oval sedge	x		x				x	x
	H	bicknellii	Bicknell's sedge	x						x	x
	H	brevior	Plains oval sedge	x							x
	H	buxbaumii	Buxbaum's sedge	x				x	x	x	
Yes	H	comosa	Bottlebrush sedge	x			x	x	x		
	H	conoidea	Openfield sedge	x				x		x	x
	H	crinita	Fringed sedge	x	x			x	x	x	
	H	cristatella	Crested sedge	x				x		x	
Yes	H	emoryi	Riverbank tussock sedge	x							
	L	haydenii	Hayden's sedge	x				x		x	
Yes	H	hystericina	Porcupine sedge	x		x		x	x	x	
Yes	H	interior	Inland sedge	x	x	x			x	x	
	L	intumescens	Greater bladder sedge	x	x			x			
	H	lacustris	Lake sedge	x			x	x		x	
	H	laeviconica	Plains slough sedge	x				x		x	
	H	laevivaginata	Smooth-sheath sedge	x	x	x			x		
	H	lasiocarpa	Wiregrass sedge	x			x	x	x	x	
	L	leptalea	Bristle-stalked sedge	x	x			x	x		
	L	lupulina	Hop sedge		x			x		x	
	M	normalis	Spreading oval sedge	x	x					x	x
Yes	H	pellita	Woolly sedge	x		x		x	x	x	
	H	prairea	Prairie sedge	x		x		x		x	
	H	sartwellii	Running marsh sedge	x		x	x	x	x		
Yes	H	scoparia	Pointed broom sedge	x				x	x	x	
	M	sterilis	Dioecious sedge	x		x			x		

Yes	M	stipata	Prickly sedges	x				x	x	x	
Yes	H	stricta	Tussock sedge	x				x	x		
	H	tenera	Narrowed-leaved oval sedge	x	x					x	x
	H	tetanica	Rigid sedge	x		x		x	x	x	
	L	tribuloides	Blunt broom sedge	x	x			x		x	
Yes	H	trichocarpa	Hairy-fruited sedge	x				x	x	x	
	H	utriculata	Swollen-beaked sedge	x				x		x	
	L	vesicaria	Lesser bladder sedge	x	x			x		x	x
Yes	M	vulpinoidea	Brown fox sedge	x	x			x	x	x	

Plugs for Shea wetlands and stream restoration					
Water depth	Water chem preference	Substrate & flow			
M		muddy soil	Alisma (plantago-aquatica) subcordatum	southern water-plantain	seed
M		muddy soil	Alisma triviale	northern water-plantain	seed
S			Carex aquatilis	water sedge	plants
M-D			Carex lacustris	lakeshore sedge	plants
S-M			Carex stricta	tussock sedge	plants
M			Carex trichocarpa	hairy-fruit river sedge	plants
S			Carex utriculata	beaked sedge	plants
S-M		marsh/stream	Cicuta bulbifera	bulblet water-hemlock	plants
S-M			Cyperus strigosus	false nut-sedge	plants
S-D	neutral		Eleocharis palustris	creeping spike-rush	plants
S	very hard		Iris virginica var. shrevei	blue flag	plants
M-D	neutral	muddy sediment	Pontederia cordata	pickerelweed	plants
M			Sagittaria brevirostra	short-beaked arrowhead	plants
M	soft	stream/muddy soil	Sagittaria latifolia	common arrowhead	plants
M	hard		Sagittaria rigida	sessile-fruited arrowhead	plants
S-D	very hard	sediment	Scirpus (Bolboschoenus) fluviatilis	river bulrush	plants
D	very hard	firm substrate/ water movement	Scirpus (Schoenoplectus) acutus	hard-stem bulrush	plants
M-D	very hard		Scirpus americanus (Schoenoplectus pungens)	common three-square	plants
S-D	hard	mucky soil	Scirpus validus (Schoenoplectus tabernaemontani)	soft-stem bulrush	plants
S		muddy soil	Sparganium americanum	American bur-reed	plants
S		muddy soil	Sparganium eurycarpum	common bur-reed	plants
S =	<6"				
M =	6-12"				
D =	>12"				

Attachment E: General References



Natural Resources Conservation Service

CONSERVATION PRACTICE STANDARD

COVER CROP

CODE 340

(ac)

DEFINITION

Grasses, legumes, and other forbs planted for seasonal vegetative cover.

PURPOSE

This practice is applied to support one or more of the following purposes:

- Reduce sheet, rill, and wind erosion
- Maintain or increase soil organic matter quantity
- Improve soil aggregate stability, soil organic matter quality, and habitat for soil organisms
- Reduce water quality degradation by utilizing excess soil nutrients
- Reduce weed and plant pest pressure
- Improve moisture management
- Reduce soil compaction
- Supply nitrogen to the subsequent crop
- Improve habitat for pollinators, beneficial organisms, or natural enemies of crop pests

CONDITIONS WHERE PRACTICE APPLIES

All lands requiring seasonal vegetative cover for natural resource protection or improvement.

CRITERIA

General Criteria Applicable to All Purposes

Cover crops are established as part of a cropping system between production crops. In addition, cover crops may also be interseeded into production crops or planted in the alleyways of perennial tree or vine crops. Select species and planting dates that will not adversely affect crop yield or interfere with the harvest process.

Plant species, seedbed preparation, seeding rates, seeding dates, seeding depths, fertility requirements, and planting methods will be consistent with applicable local criteria and soil/site conditions. Determine the method and timing of termination to meet the grower's objective and the current NRCS Cover Crop Termination Guidelines.

Cover crops must be compatible with other components of the cropping system such as crops, available equipment, and timing of operations.

Ensure chemical applications used with previous crops and for the establishment of the cover crop are compatible with cover crop selections and purposes.

Do not burn cover crop residue

Do not mechanically harvest cover crops for seed, hay, silage, or other biomass.

If the specific rhizobium bacteria for the selected legume are not present in the soil, treat the seed with the appropriate inoculum.

Seed will be free of noxious weed seed.

Additional Criteria to Reduce Sheet, Rill, and Wind Erosion

Time the cover crop establishment in conjunction with other practices to adequately protect the soil during the critical erosion periods.

Select cover crops that will have the physical characteristics necessary to provide adequate erosion protection.

Use the current erosion prediction technology to determine the amount of surface and canopy cover needed from the cover crop to achieve the erosion objective.

Additional Criteria to Maintain or Increase Soil Organic Matter Quantity

Select cover crop species that produce high volumes of aboveground biomass and root mass to maintain or increase soil organic matter.

The planned crop rotation including the cover crop and associated management activities will score a Soil Conditioning Index (SCI) value > 0 , as determined, using the current approved NRCS SCI procedure, with appropriate adjustments for additions to and subtractions from plant biomass.

Plant the cover crop as early as possible and terminate as late as practical to maximize plant biomass production, while considering the time needed to prepare the field for planting the next crop, and soil moisture depletion.

When utilizing livestock, graze at later stages of maturity in order to maximize root biomass and to allow for at least 50% of the total aboveground vegetation to remain with the majority to be flattened onto the soil surface.

Additional Criteria to Improve Soil Aggregate Stability, Habitat for Soil Organisms and Organic Matter Quality

To improve soil aggregate stability, select cover crops that contain at least one fibrous rooted grass in conjunction with other practices in a soil health management system to bind aggregates and support aggregate-building soil organisms

To Improve Habitat for Soil Organisms and Organic Matter Quality, seed a minimum of 5 species of plants that includes at least one grass, one legume, and one other broadleaf in conjunction with other practices in a soil health management system to provide a supply of diverse soil organism food.

Include plants with diverse root systems which, in conjunction with other practices in the soil health management system, will increase the SCI OM subfactor by 0.05 or greater.

Additional Criteria to Reduce Water Quality Degradation by Utilizing Excess Soil Nutrients

Establish cover crops as soon as practical prior to or after harvest of the production crop.

Select cover crop species for their ability to effectively utilize nutrients.

Terminate the cover crop as late as practical to maximize plant biomass production and nutrient uptake.

Additional Criteria to Reduce Weed Pressures and Break Pest Cycles

Select cover crop species for their life cycles, growth habits, and other biological, chemical, and physical characteristics to provide one or more of the following:

- Suppress or compete with weeds
- Break pest life cycles or suppress pests, including pathogens
- Provide food or habitat for natural enemies of pests
- Release compounds such as glucosinolates that suppress soilborne pathogens or pests

Select cover crop species that do not harbor unmanageable pests or diseases of subsequent crops.

Additional Criteria to Improve Moisture Management

In areas of limited soil moisture, terminate growth of the cover crop sufficiently early to conserve soil moisture for the production crop. Leave residues of cover crops on the soil surface.

In areas of potential excess soil moisture, allow the cover crop to grow as long as possible to maximize soil moisture removal.

Additional Criteria to Reduce Soil Compaction

Select cover crop species that can penetrate or prevent compacted layers.

Additional Criteria to Supply Nitrogen to Subsequent Crop

Legumes (with appropriate inoculants where necessary), either alone or in a seed mix, are used to improve fertility by providing the subsequent crop with a minimum of 20% but not more than 100% of the crop's estimated nitrogen requirement.

Use land grant university (LGU's) publications or cover crops analysis to estimate the amount of nitrogen in the cover crop. The nitrogen credits from the cover crop must be accounted for in the nutrient budget for the subsequent crop.

Use LGU's publications or field data to determine the effects of termination timing and termination methods (which may include incorporation, grazing, crimping, mowing or agrichemicals) on the amount of estimated available nitrogen for the subsequent crop..

Additional Criteria to Improve Habitat for Pollinators, Beneficial Organisms, or Natural Enemies of Crop Pest

Use cover crop mixes that contain at least 50% forbs of known habitat, pollen, or nectar value to targeted pollinators or other beneficial insects that attack crop pests. Allow these forbs to achieve at least 50% bloom before termination.

Cover crop seeds must not be treated with systemic insecticide coatings that may pose a risk to beneficial organisms. Cover crops must not be exposed to pesticide sprays, seed coatings, or drift that can negatively impact the targeted pollinators or beneficial organisms. [See Agronomy Technical Note 9 for determining potential impacts.]

CONSIDERATIONS

General Considerations

Plant cover crops in a timely manner and when there is adequate moisture to establish a good stand.

Avoid cover crop species that harbor or carry over potentially damaging diseases or insects.

Cover crops may be used to improve site conditions for establishment of perennial species by providing early cover for emerging perennial seedlings. In such cases, meeting a primary purpose still applies.

When cover crops are used for grazing, select species that will have desired forage traits, be palatable to livestock, and not interfere with the production of the subsequent crop.

Cover crops residues should be left on the soil surface to maximize mulching (physical) effects.

Cover crops, flattened to the soil surface can moderate soil temperatures, keeping soils cooler during hotter periods and warmer during cooler periods.

Cover crops can be selected and managed for allelopathic effects. Evaluate potential allelopathic effects to the subsequent crop.

Cover crops may be selected that release biofumigation compounds that inhibit soilborne plant pests and pathogens.

Seed a higher density cover crop stand to promote rapid canopy closure and greater weed suppression. Increased seeding rates (1.5 to 2 times normal) can improve the cover crop competitiveness with weed species.

Species can be selected to serve as trap crops to divert pests from production crops.

Select a mixture of two or more cover crop species from different plant families to increase soil biological diversity or to provide food and cover for wildlife habitat.

Select cover crop species or mixture, and timing and method of termination that will maximize efficiency of nitrogen utilization by the following crop, considering soil type and conditions, season and weather conditions, cropping system, carbon (C) to nitrogen (N) ratio of the cover crop at termination, and anticipated nitrogen needs of the subsequent crop.

To ensure timely seeding of cover crops, employ planting methods that allow for early season growth such as interseeding or broadcast overseeding into standing crops.

Time the termination of cover crops to meet nutrient release goals. Termination at early vegetative stages may cause a more rapid release compared to termination at a more mature stage.

Both residue decomposition rates and soil fertility can affect nutrient availability following termination of cover crops. As an example, higher C to N plant residues in conjunction with lower soil fertility could slow the availability of N to growing plants.

Use diverse cover crop species mixtures with various C:N ratios or maturity that upon decomposition allow nutrients to be released throughout the growing season of the next crop, enhancing nutrient cycling and nutrient retention.

Legumes add the most plant-available N if terminated when about 30 - 50 percent of the crop is in bloom (depending on species) .

Avoid cover crop species in situations where cover crop seed can contaminate production crops

Cover crops can reduce pesticide losses by reducing erosion and adding organic matter.

Cover crop species selected for their ability to effectively utilize potential water quality degrading nutrients may also be used to conserve and cycle other nutrients as well.

When appropriate, refer to crop insurance criteria when deciding the timing of cover crop termination.

Considerations to Reduce Sheet, Rill, and Wind Erosion

Maximize the combined canopy and surface residue cover to attain a minimum of 90-percent cover during the period of potentially erosive wind or rainfall.

Considerations to Maintain or Increase Soil Organic Matter Quantity

Increase the diversity of cover crops (e.g., mixtures of several plant species or functional groups) to promote a wider diversity of soil organisms, and possibly promote increased soil organic matter.

Plant legumes or mixtures of legumes with grasses, brassicas, and other forbs to provide N through biological N fixation.

Considerations to Improve Soil Health

In semiarid regions, where seasonal fallow is used, consider leaving sufficient residues to protect the soil surface during the fallow period, or growing a shallow-rooted cover crop that allows deep moisture storage. Reduce the intensity of tillage and increase soil surface coverage with vegetation and crop residues.

When applying agrichemicals, consider the potential impact on the soil organisms and consult with a pesticide professional to develop alternative application techniques or alternative agrichemicals that have lower adverse impacts on soil organisms.

Select diverse cover crops that have shallow, medium, and deep roots to maximize aggregate stability, to increase organic matter, and to improve water infiltration and improve soil structure.

The effects of this practice can be enhanced by being integrated into a soil health management system. Refer to Technical Note 450-4 for more information.

With increasing water infiltration due to improved soil health, ephemeral gully occurrences can be minimized.

The effects of this practice can be enhanced by utilizing animal wastes, or applying nonsynthetic mulches to supplement the biomass produced by cover crops.

Considerations to Reduce Water Quality Degradation by Utilizing Excess Soil Nutrients

Use deep-rooted species to maximize nutrient recovery.

When appropriate for the cropping system, mowing certain grass cover crops (e.g., sorghum-sudangrass, pearl millet) prior to heading and allowing the cover crop to regrow can enhance rooting depth and density.

PLANS AND SPECIFICATIONS

Develop plans and specifications for each field or treatment unit according to the criteria and operation and maintenance requirements of this standard. Specifications must describe the requirements to apply the practice to achieve the intended purpose. Record the following specification components in an approved CPS Cover Crop (Code 340) implementation requirements document:

- field number and acres

- species of plants to be established
- seeding rates
- seeding dates
- seeding depth
- establishment procedure including planting method
- rates, timing, and forms of nutrient application (if needed)
- dates and method to terminate the cover crop
- other information pertinent to establishing and managing the cover crop

OPERATION AND MAINTENANCE

Evaluate the cover crop to determine if the cover crop is meeting the planned purposes. If the cover crop is not meeting the purposes, adjust the management.

REFERENCES

Chessman, D., B.N. Moebius-Clune, B.R. Smith, B. Fisher. 2019. The Basics of Addressing Resource Concerns with Conservation Practices within Integrated Soil Health Management Systems on Cropland. Soil Health Technical Note No. 450-04. U.S. Department of Agriculture, Natural Resources Conservation Service.

Clark, A. (ed.). 2007. Managing cover crops profitably. 3rd ed. Sustainable Agriculture Network Handbook Series; bk 9.

Hargrove, W.L., ed. Cover crops for clean water. SWCS, 1991

Magdoff, F. and H. Van Es. Cover Crops. 2000. p. 87-96 *In* Building soils for better crops. 2nd ed. Sustainable Agriculture Network Handbook Series; bk 4. National Agriculture Library. Beltsville, MD.

Reeves, D.W. 1994. Cover crops and erosion. p. 125-172 *In* J.L. Hatfield and B.A. Stewart (eds.) Crops Residue Management. CRC Press, Boca Raton, FL.

NRCS Cover Crop Termination Guidelines:

<http://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/climatechange/?cid=stelprdb1077238>

Revised Universal Soil Loss Equation Version 2 (RUSLE2) Website:

<http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/tools/rusle2/>

Wind Erosion Prediction System (WEPS) Website:

<http://www.nrcs.usda.gov/wps/portal/nrcs/main/national/technical/tools/weps/>

USDA, Natural Resources Conservation Service, National Agronomy Manual, 4th Edition, Feb. 2011. Website: <http://directives.sc.egov.usda.gov/>

Review

Soil Oxidation-Reduction in Wetlands and Its Impact on Plant Functioning

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Abstract: Soil flooding in wetlands is accompanied by changes in soil physical and chemical characteristics. These changes include the lowering of soil redox potential (Eh) leading to increasing demand for oxygen within the soil profile as well as production of soil phytotoxins that are by-products of soil reduction and thus, imposing potentially severe stress on plant roots. Various methods are utilized for quantifying plant responses to reducing soil conditions that include measurement of radial oxygen transport, plant enzymatic responses, and assessment of anatomical/morphological changes. However, the chemical properties and reducing nature of soil environment in which plant roots are grown, including oxygen demand, and other associated processes that occur in wetland soils, pose a challenge to evaluation and comparison of plant responses that are reported in the literature. This review emphasizes soil-plant interactions in wetlands, drawing attention to the importance of quantifying the intensity and capacity of soil reduction for proper evaluation of wetland plant responses, particularly at the process and whole-plant levels. Furthermore, while root oxygen-deficiency may partially account for plant stress responses, the importance of soil phytotoxins, produced as by-products of low soil Eh conditions, is discussed and the need for development of methods to allow differentiation of plant responses to reduced or anaerobic soil conditions vs. soil phytotoxins is emphasized.

Keywords: flooding; photosynthesis; plant stress; soil redox potential; soil phytotoxins; wetlands

1. Introduction

Excess water in wetland soils is a major factor affecting plant survival and functioning. In saturated soils, the supply of atmospheric oxygen into the soil is curtailed and various facultative and obligate anaerobic microorganisms use oxidized compounds as electron acceptors for respiration, thus converting them to reduced forms. The reduction and the associated processes influence plant survival, growth and functioning in wetlands. This review focuses on the literature relevant to this topic and the need for development of research methods associated with properly quantifying of soil reduction processes that can aid in the evaluation of plant responses in wetland environments.

2. Soil Oxidation-Reduction

A chain of reactions is initiated upon soil flooding leading to reduced (low) soil redox potential (Eh, mV) conditions. These reactions include physical, chemical and biological processes that have significant implications for wetland plants [1–3]. Physical processes include restriction of atmospheric gas diffusion in the soil leading to depletion of soil oxygen and accumulation of carbon dioxide [4,5]. Shortly after flooding, the limited supply of oxygen in soil pore spaces is depleted rapidly by roots, microorganisms, and soil reductants [6]. This process leads to oxygen depletion and reduction in soil oxidation reduction potential (Eh) followed by a chain of soil chemical changes. The processes that follow include denitrification, reduction of iron, manganese and sulfate, and changing soil pH and Eh [3]. For example, in a typical series of reductions NO_3^- is reduced to N_2 , Mn^{+4} to Mn^{+2} , Fe^{+3} to Fe^{+2} , SO_4^{2-} to H_2S , S^{2+} or HS^- (depending upon pH) and accumulations of acetic and butyric acids that are produced by microbial metabolism [1,2].

3. Quantifying Soil Redox Potential Conditions

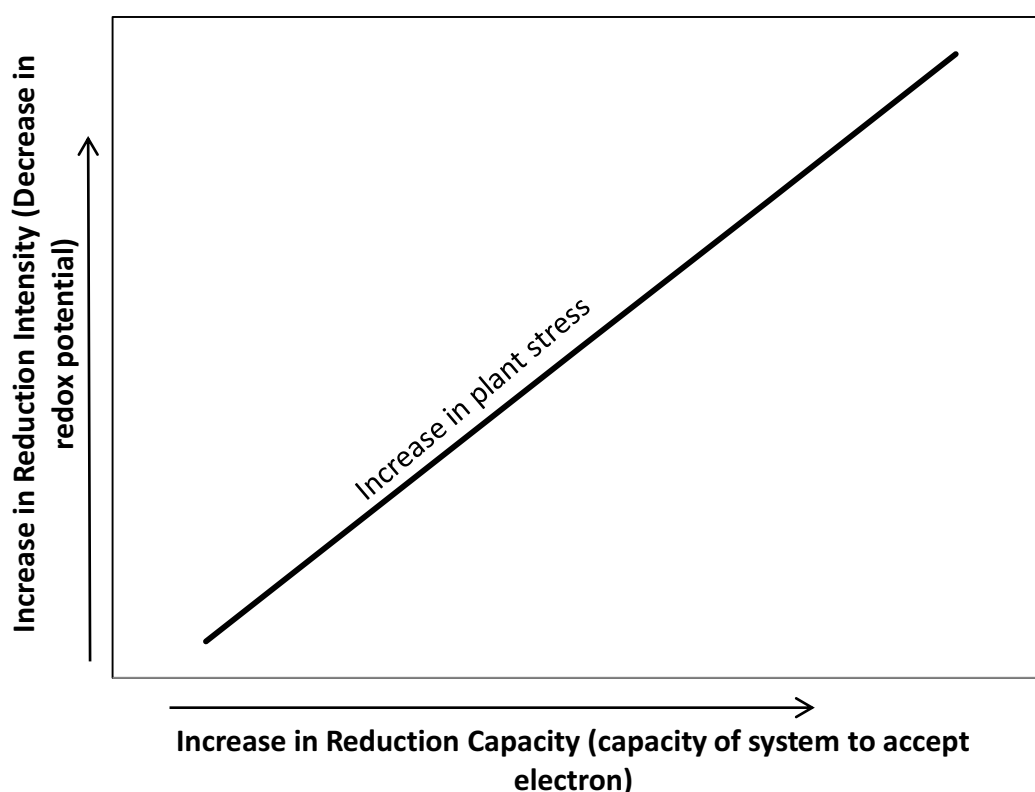
Review of literature reveals that many terms such as “flooded”, “saturated”, “waterlogged” are utilized to describe oxygen-deficient root medium. Obviously, these terms are qualitative and do not quantitatively define the rhizosphere [7]. Furthermore, methods used to quantify oxygen content and oxygen diffusion rate in drained soils cannot be employed effectively in wet soils [3]. In contrast, measurement of soil Eh is a valuable tool because it can be measured in laboratory and in the field (for details see [8,9] and the references cited therein). Furthermore, quantifying soil Eh is particularly advantageous in periodically flooded soils since the range of Eh is much wider, between approximately –300 to +700 mV, than either aerated (Eh > +400 mV) or permanently waterlogged (Eh < +350 mV) soils [10–12]. Thus, soil Eh or redox measurements represent an excellent quantifying tool for defining the presence or absence of oxygen and the soil chemical status in wetland soils.

4. Intensity and Capacity of Soil Reduction

In wetland soils, the oxidation-reduction is used to signify the intensity of reduction. However, the reduction of inorganic redox systems including oxygen following flooding can be described in “intensity” and “capacity” terms [7]. Although critical Eh values (intensity of reduction) at which the inorganic redox systems become unstable do provide valuable information, they do not provide any indication of the total capacity of the system to accept electrons, supporting respiration or oxygen

demand in the root zone [9]. In contrast, redox capacity represents the amount of electrons accepted by oxidants (such as oxygen, nitrate, manganese, iron, and sulfate) supporting respiratory of microorganism decomposing organic matter. The oxidants may have a relative high redox buffering capacity which explains why some wetland soil with relatively large amount of bio-reducible iron do not undergo a rapid decrease in redox potential (intensity) following flooding. High soil reduction capacity at any intensity of reduction in the root zone can compete for oxygen transported thru aerenchyma into the root rhizosphere and potentially can increase plant stress above that caused by intensity of reduction alone (Figure 1).

Figure 1. Oxidation-reduction potential in wetland soils: relationship of intensity and capacity of reduction in soil to wetland plant stress.



The intensity factor determines the relative ease of the reduction, while the capacity factor denotes the amount of redox system undergoing reduction, e.g., oxygen consumption at root interface [7,13,14]. This relationship may be expressed as follows: $E_h = E_o + 2.3 \left[\frac{RT}{nF} \right] \log_e \left[\frac{Ox}{Red} \right]$; where Ox and Red are the concentrations of the oxidized and reduced forms, respectively, of the substance under consideration, E_o is the electrode potential of the 50% oxidized system specific to that substance, n is the number of moles of electrons transferred, F is the Faraday constant, R is the gas constant, and T is the temperature (K) [12]. It then follows that E_h is dependent on the ratio of oxidized and reduced forms and not on their absolute quantities. Therefore, a 90% oxidized system has the same electrode potential no matter whether the total concentration is 0.01% or 10%, but the poisoning (capacity) of the latter will be 1000 times greater. Thus, a system of $E_o + 0.1$ volt will oxidize a system of $E_o - 0.1$ volt, but will be oxidized by a system of $E_o + 0.3$ volts; however, the extent to which the reactions will take place depend upon the capacity of the systems.

The redox capacity factor is important although less is known about whether it is the intensity or the capacity that is most affecting plant functioning. As noted above, two soils with the same level of intensity of reduction may differ substantially in the capacity for reduction. The reduction capacity is estimated using measurements of soil respiration and calculating oxygen equivalent by stoichiometry [14]. However, part of the oxygen consumption is due to microbial respiration and partly due to direct oxidation of the accumulated reductants. Development of methodology for distinction of these two components therefore, is needed. In the laboratory, levels of soil redox capacity may be created and/or manipulated by adding extra carbon (organic matter) as energy source to the soil while maintaining the redox intensity level. In an experimental set up, reduction capacity may be controlled by adding granular D-glucose to the growth medium that is maintained under set redox intensity conditions [15].

To properly evaluate wetland plant responses to soil flooding, both intensity and capacity of soil reduction must be quantified because these two components influence oxygen demand in the soil [7,14]. Kludze *et al.* [16,17] and Sorrell *et al.* [18] using titanium citrate solution to create a high O₂-demand in root environment, reported that root oxygen transport and release were affected by such conditions in several wetland species. However, such a solution, while a significant improvement over de-oxygenated solution, at best only mimics wet soil conditions [14] and does not represent other important characteristics of wet soils, such as soil capacity for phytotoxin production that may have significant adverse effects on many wetland plants.

5. Soil Reduction and Wetland Plant Functioning

Responses of plants to low oxygen in the root zone have been typically assessed by growing plants hydroponically, then introducing pressurized nitrogen through the solution to remove oxygen [7]. In such a system, roots are exposed to Eh only slightly below values where oxygen disappears on the redox scale (*i.e.*, +350 to +400 mV; [7]). However, low oxygen conditions are represented by Eh values ranging between +400 and −300 mV. The Eh around −300 mV may occur in highly reduced soils. Since oxygen is absent at Eh values beginning at or below +350 mV, the absence of oxygen alone does not provide much information on the intensity of reduction. Furthermore, studies designed to evaluate responses of plants grown at the upper portion of the anaerobic range of the redox scale may yield results that are not typically the same as those displayed by plants growing in a more reducing environments.

Based on the considerations outlined above, it is argued that the common laboratory approaches of pressurized N₂ may be sufficient for evaluation of responses of flood-sensitive plants, such as many crop species, to low oxygen conditions. However, evaluation of responses of wetland plants to oxygen-deficient soils require methods that represent root zone reduction at levels at which flood-tolerant wetland species are subjected to in natural wetland soil environment. These plants can survive low to extreme reducing conditions covering a significant portion along the redox scale in their natural environments.

Clearly, in wetland soils, plants are faced with not only the lack of oxygen but a substantial demand for oxygen in the sediment due to plant roots and microbial demand [7,9,13,19–26]) that is represented by low soil Eh. Extensive field data on the relationship between Eh and plant community distribution in saltmarshes were presented by Armstrong *et al.* [27]. Pennington and Walters [28] and Davy *et al.*

[29] reported sediment Eh as a major factor affecting survival and growth of their study species. It is known that in sediments characterized by weak redox capacity, certain wetland plants are capable of increasing the Eh of the bulk sediment [30–32].

In a typical flooded soil, plants may respond to soil physicochemical changes by displaying a wide range of stress symptoms that have been reported in numerous publications (for reviews see [19,22,23,33–36]. However, due to lack of quantifying Eh conditions in many reports, the relationship between soil Eh and wetland plant functioning is less understood. From a physiological-ecology standpoint, soil Eh data provide insights into the status of various soil compounds, many of them important to wetland plant functioning. For example, a soil Eh of zero mV indicates that oxygen and nitrate are not likely to be present while the bio-reducible iron and manganese compounds are in a reduced state. Eh reading of +400 mV indicates that oxygen may be present despite the presence of excess water in the soil [7,37,38].

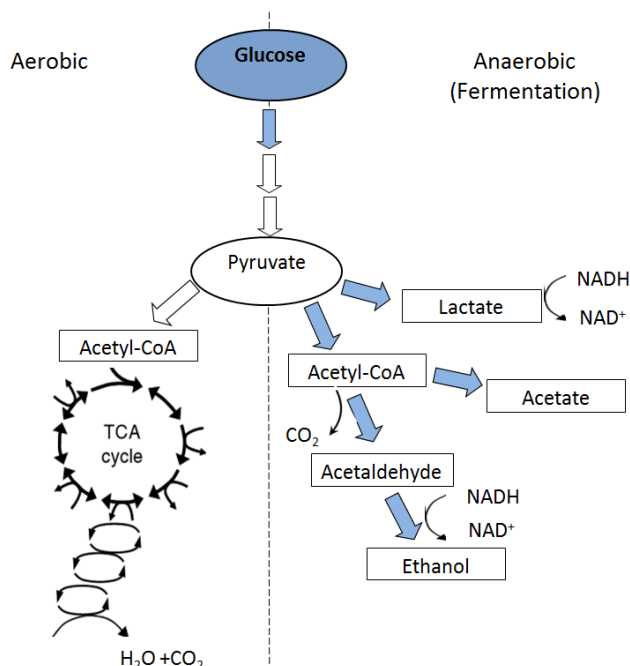
A major consequence of soil flooding and the subsequent reducing conditions is development of high competitive oxygen between root and soil microbial demand that may affect internal plant tissue oxygen concentrations thus, its critical metabolic processes [7,19,21,26,39–41]. Other consequences of soil reduction processes include changes in availability and/or concentrations of various nutrients that are essential for plant functioning, and production of a host of compounds known to be phytotoxic [3,8,42,43]. These compounds include: reduced forms of Fe and Mn, ethanol, lactic acid, acetaldehyde and aliphatic acids such as formic, acetic, butyric acids, and cyanogenic compounds [2,6,44]. The accumulation of these compounds in flooded soils may reach levels that can cause injury to plants [1,9,45]. For instance, excess soil sulfide is known to inhibit growth of various marsh macrophytes [20,21,46–48]. The soluble sulfide species including H_2S can be toxic to plant roots [38,49,50]. The organic acids such as acetic, butyric, propionic and caproic acids have a variety of adverse effects on plants [20,21,38,51,52].

In the following sections, the effects of soil flooding, and the concomitant drop in soil Eh, on certain plant metabolic processes, physiological functions, anatomical and morphological features, growth and survival is discussed.

6. Metabolic Responses to Flooding

Metabolic adaptations are complex mechanisms that allow wetland plants to survive anoxic soil conditions [8,38]. Normal growth and functioning of roots require more oxygen than is needed for root respiration processes alone [4,53]. Under aerated conditions, oxygen primarily diffuses into the roots from soil air spaces via the root epidermis. However, when roots are flooded, the presence of water column in soil creates a severe barrier to gas diffusion, thus oxygen must reach the roots through internal paths from aerial parts [38,54]. Such conditions lead to root energy deficiency because of the inhibition of normal (aerobic) root respiration. Therefore, much of the immediate flood-injury to roots is attributed to their oxygen status [4,28,55]. Under root oxygen stress, mitochondrial respiration is compromised while metabolism is shifted to fermentation. The process converts pyruvate to ethanol (Figure 2) via activity of enzyme alcohol dehydrogenase (ADH) or to lactate via activity of lactate dehydrogenase (LDH) [56].

Figure 2. Metabolic pathways under aerobic and anaerobic conditions (from Reddy and DeLaune [9]).



Increased ADH activity in response to flooding has been reported for many plants as an indicator of oxygen deficiency [57–59]. The response has been reported for flood-sensitive as well as flood-tolerant plants [60,61]. The role of ADH in flood-tolerance has been known for sometime and may include maintaining intracellular pH. The ability to survive is related to the extent of cytosolic acidosis due to accumulation of organic acids from fermentation, such as lactate. The changes in cell pH have considerable impact on cell metabolism due to reduction in activities of several enzymes that require pH close to 7 for optimum activity [62]. The ADH activity appears to be inversely related to soil Eh due to anaerobic respiration [9]. Nonetheless, it is not known if the induction of ADH activity contributes to the plant survival or signals the harmful effects of root anoxia [54].

Major products of fermentation are ethanol and CO₂. Anaerobic respiration, however, is rather an inefficient pathway of energy production because it produces 2 moles of ATP per each glucose molecule broken down to pyruvic acid compared to 36–38 ATPs generated from each glucose in aerobic respiration. The low ATP production creates an energy deficiency that affect many plant metabolic functions including water and nutrient uptake, internal solute transport, and photosynthetic carbon fixation. Additionally, the increased glucose consumption during fermentation may lead to carbohydrate depletion in plants leading to low growth. The metabolic processes affected may include reduction in activity of photosynthetic enzymes. The activity of these enzymes is highly sensitive to changes in environmental conditions [63–66]. In addition, decrease in leaf tissue chlorophyll content has been reported in response to environmental stresses including soil flooding [66,67]. Many species rely on anaerobic metabolism as a means of surviving anaerobic root conditions yielding very few molecules of ATP [4,68]. Wetland plants maintain carbohydrate reserves to support sustained ATP generation [69,70]. Thus, the carbohydrate stored in the roots may potentially play an important role in plant survival since presumably the carbohydrates can be used to feed anaerobic respiration under reduced soil Eh conditions.

The ability to survive flooding is also related to avoidance of ethanol production in glycolytic pathway. Ethanol accumulation in flood-sensitive species may lead to death of root cells, therefore, to avoid excess accumulation of ethanol, it may be leaked out of plant via transpiration stream and/or leakage as well as production of alternate end products such as malate and lactate. Reduction of water and nutrient uptake, disturbance of hormonal balance such as a decrease in gibberellin and cytokinin and an increase in abscisic acid and ethylene [71] due to flooding has been reported in the literature [72,73].

7. The Internal Oxygen Transport System

Root and rhizomes in flooded wetland plants obtain oxygen via gas-phase transport from the shoot system, internal photosynthetic oxygen production, or atmospheric oxygen through an extensive oxygen transport system (aerenchyma tissue) in roots, stems, and leaves [17]. This system allows a plant to transport the needed oxygen to the roots for maintaining aerobic respiration and to oxidize reducing compounds in the rhizosphere, thus establishing a gradient of soil oxygen availability. The role that roots of certain wetland woody species have on establishing such radial gradients in a soil profile that influences soil redox status has been reported by several researchers [74–76]. However, the development of morphological and anatomical features in response to flooding in most plants is time dependent. Thus, during the initial period of stress, the required energy for survival is mostly generated through anaerobic metabolism [4,63].

The internal system of large gas spaces reduces internal volume of respiring tissues and oxygen consumption, thus, enhancing the potential for oxygen reaching the distant underground portions of the plant [17,20,21]. Because of the advantages, the oxygen transport system has been considered as a major mechanism critical to plant's ability to cope with soil anoxia [17,19–21,28–30,50,77–82]. Diffusion, while the major pathway of root aeration in wetland plants, is not the only means, as rhizome ventilation due to pressurized throughflows of gases has been demonstrated for some species [20,21,83,84].

The effectiveness of the gas transport is primarily dependent on two factors: (1) the resistance to diffusion that is proportional to root length and inversely proportional to root porosity; and (2) the oxygen demand along the diffusion path resulting from respiratory needs as well as oxygen leakage from the roots into the rhizosphere [49,85]. Indeed, oxygen demands of roots and rhizosphere, which may include large communities of facultative anaerobes, are competitive for oxygen molecules because in reduced soils these systems compete for the plant pool of oxygen simultaneously [19,79,84]. As soil reduction continues, there is a progressively greater demand imposed upon roots for oxygen [7].

It is known that Eh conditions and microbial oxygen demand in the soil are among major factors affecting root oxygen release to the rhizosphere [26]. However, literature concerning the relationship between functional aspects of gas transport within plants and soil Eh conditions is limited. In a few studies that evaluated the relationship, it is evident that intense soil reduction promotes oxygen loss from root to the rhizosphere. For instance, high correlation was found between radial oxygen loss rates from roots and soil Eh intensity; there was an increasingly higher oxygen loss rates as soil Eh became more reduced [14]. However, the enhancement may require soil Eh below some threshold levels [86]. It is reported that in *Spartina patens*, a dominant US Gulf coastal brackish marsh species, root porosity

increased as sediment Eh decreased, leading to root porosity of 22% in plants grown at +200 mV while porosity was 45% in plants grown at −300 mV Eh. Radial oxygen loss was significantly greater for plants grown in −300 mV Eh compared to plants grown at +200 mV Eh [87]. Other studies have shown similar patterns of responses for root porosity-soil Eh intensity relationship in wetland plants including swamp and bottomland woody species [17,88]. In contrast, Brix and Sorrell [89] reported that root porosity in two wetland species, *Phalaris arundinacea* and *Glyceria maxima*, did not change in response to a short-term (7–12 days) reducing Eh in root medium.

Despite the reported increase in aerenchyma tissue formation (and hence porosity) in wetland species in response to reducing Eh conditions, this enhancement may not be sufficient to satisfy the root respiratory needs for oxygen due to the greater radial oxygen loss rates in response to high intensity of reduction. Pezeshki *et al.* [90,91] concluded that despite a substantial enhancement of aerenchyma tissue formation in *Spartina patens*, alcohol dehydrogenase (ADH) activity continued to be higher in flooded than control plants indicating continued oxygen stress in the roots of flooded plants.

In addition to the effects of the intensity of reduction, differences in Eh capacity among wetland soils may influence many plant functions including oxygen transport, rhizosphere oxygenation, and, thus, many aspects of plant functioning [13,14]. Studies showed that increased Eh capacity under a constant Eh intensity did not have any significant effect on root porosity in *S. patens* but oxygen release from roots to the rhizosphere was increased in response to the increasing Eh capacity [14]. However, the authors reported that there was a threshold Eh capacity beyond which oxygen release remained constant and/or decreased in this species. The response was attributed to the potential effects of several factors such as soil phytotoxins as well as stomatal closure. Nonetheless, the reason(s) for such a response remains unknown.

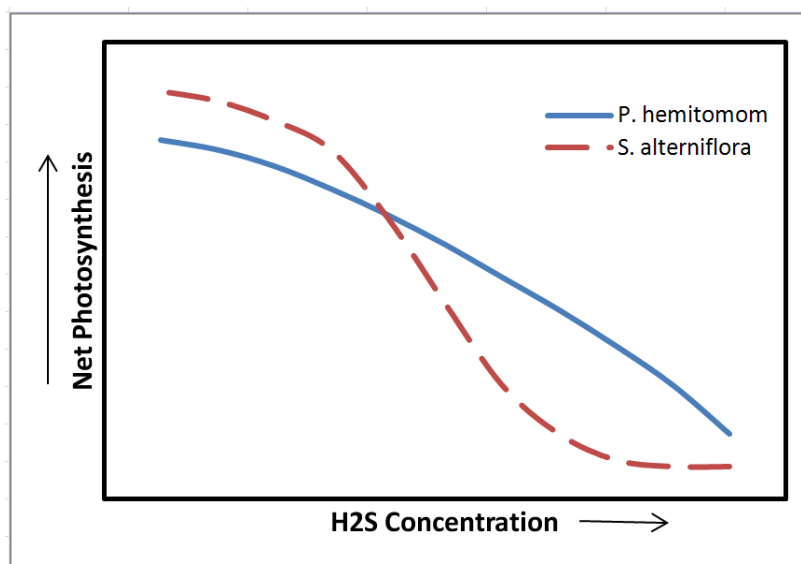
8. Plant Nutrition

Plant nutrition is influenced by soil flooding and the processes associated with reducing soil Eh conditions. Many factors including soil physicochemical characteristics, nutrient pools, plant developmental and physiological status, and flood-tolerance capabilities are important [22,78,92]. Despite the adaptations reported for wetland plants, various nutritional deficiencies and toxicities may occur. Reduced soil conditions may lead to inhibition of nutrient uptake and transport due to root dysfunction, death [22,61,93,94] and blockages in the vascular and aerenchyma systems resulting from phytotoxin damages [20]. Oxygen supplies to the roots are critical for nutrient uptake and ion transport. Flood-induced stress include reduced water uptake due to root dysfunction that results from soil O₂-deficiency including altered cation and anion concentration in xylem sap as well as decreased hydraulic conductance of roots has been reported in the literature for many species [95,96]. The generation of adequate ATP is an important requirement for active uptake that occur via the H⁺ translocating ATPase in the plasma membrane [43]. Jackson *et al.* [96] reported that flooding degraded root integrity within 10 hours of initiating treatment in tomato plants and solute uptake was deregulated. DeLaune *et al.* [93] using add labeled N-15 measured uptake in cherrybark oak (*Quercus falcata* var. *pagodaefolia*) and overcup oak (*Q. lyrata*) and reported decreased N-15 uptake under moderate reducing soil conditions as compared to oxidized conditons

There are ample reports of reduction of water and nutrient uptake, disturbance of hormonal balance such as a decrease in gibberellin and cytokinin and an increase in abscisic acid and ethylene in response to flooding [71–73]. Under reduced soil conditions, some wetland plants may continue ion uptake partly because of the internal O_2 supply system but partial anoxia in roots can reduce solute intake [43,61,97]. Nutrient concentrations at toxic levels may be accumulated in tissues under reduced conditions due to higher availability of certain nutrients and root dysfunction [9,98,99]. During prolonged flooding, as soil Eh reduction continues, pH decreases while zinc availability increases leading to high tissue zinc concentrations [100] and reduced ferric and manganic forms that are soluble [6]. Thus, tissue Mn and Fe concentrations are greater than found in plants under aerated conditions [101–103]. Leaf discoloration (bronzing) due to high soluble ferrous iron has been reported in some species [49].

Further soil Eh reduction leads to reduction of sulfate to sulfide by anaerobic microorganisms [104]. Although sulfide is phytotoxic, in most cases wetland plants have the capability to oxidize sulfide in the rhizosphere thus, avoiding or minimizing injury [49]. However, there are several reports confirming that excess soil sulfide may inhibit plant growth [20,21,46–48]. The soluble sulfide species including H_2S are toxic to the roots [49,50]. For instance, sulfate uptake, translocation and accumulation in foliage is documented for several species [105,106]. The inhibitory effect of H_2S on cytochrome oxidase is disruptive for aerobic respiration and excess cytosolic Fe and Mn is harmful to enzymatic structures [33]. The inhibitory effects of elevated sulfide concentrations on leaf photosynthetic capacity have been demonstrated in several wetland species including *Panicum hemitomom* and *Spartina alterniflora* (Figure 3, Pezeshki *et al.* [99,107]. Such photosynthetic response has been attributed to disruption of light reactions [108] and/or photophosphorylation [109], and alterations in activity of photosynthetic enzymes [110–112]. Sulfide utilization and injuries have been reported in hypoxic roots and rhizomes of *Phragmites australis* [113]. Sulfide has been implicated as a factor responsible for decreased plant growth and productivity in several wetland species [20,21,99,114].

Figure 3. The relationship between net photosynthesis and H_2S concentration in the sediment for two wetland species, *Panicum hemitomom* and *Spartina alterniflora* (from Pezeshki *et al.* [99,107].



9. Plant Water Relations and Gas Exchange

Factors associated with low soil Eh conditions can influence plant water relations through stomatal closure and slower water uptake than under aerated conditions [23,95,96,115–118]. Increased internal water stress and leaf dehydration leading to stomatal closure have been reported in some species due to a decrease in root permeability when roots were flooded [23,78,119]. Reduced water uptake due to root dysfunction may include altered cation and anion concentration in xylem sap. Decreased hydraulic conductance of roots has been reported in the literature for many species [95,96].

The extent of development of internal water stress reported for some species shows a wide range, however, in most cases the initial stomatal closure occurs in the absence of significant changes in plant water status [120–122]. The rapid stomatal closure and maintenance of a favorable water status thus, is likely due to low transpiration rates for which a slow water absorption rate by roots may sufficiently compensate rather than a sustained root conductivity [123,124]. Else *et al.* [116] found that in some species, flooded roots led to rapid stomatal closure via a root-shoot signaling mechanism, thus avoiding the possibility of dehydration. Many wetland species initially close stomata in response to soil flooding, however, exceptions have been reported in the literature. For instance, stomata in certain mangroves did not respond to Eh as low as -180 mV over short-term experimental exposures [125,126]. The stomatal closure is concomitant with a reduction in photosynthesis. However, under prolonged soil reduction stomatal reopening may occur leading to photosynthetic recovery [127]. The degree of resumption of stomatal functioning appears to be dependent on species, duration of reducing conditions, and the intensity of soil reduction.

Decreases in photosynthetic rates have been reported for some species in response to reducing soil Eh conditions; Figures 4, 5 [23,28,81,82,117,128]. For example, DeLaune *et al.* [7] studied photosynthetic responses to soil Eh using Titanium-citrate solution. The authors noted that the intensity of reduction in growth medium had significant influence on plant photosynthetic activity in marsh grass *Spartina patens* as Eh below -200 mV led to decreased photosynthesis. Krauss *et al.* [128] noted decreased stomatal conductance and net photosynthesis for baldcypress (*Taxodium distichum*) plants flooded in a greenhouse. As soil Eh dropped to -40 to -70 mV range, stomatal conductance reduced 36% and net photosynthesis dropped 40% compared to controls. In general, reducing soil Eh conditions adversely impact photosynthetic rates in wetland plants (Figure 6) although the extent of the impact varies across species as shown in Table 1. Additional studies by Pennington and Walters [28], Gravatt and Kirby [129], and Krauss *et al.* [128] have further confirmed the inhibitory effects of low soil Eh on photosynthesis of woody species. The photosynthetic decline may be attributed to a combination of diffusional limitations on gas exchange due to stomatal closure and metabolic (non-stomatal) inhibition [127]. However, the contribution of each component requires further assessment. In response to low soil Eh in range of -200 to $+100$ mV, a shift in light response curves was noted in some woody species suggesting the adverse effects of low Eh on the photosynthetic capacity of the leaves [88].

Figure 4. Changes in net photosynthesis of *Typha domingensis* in response to soil redox conditions. Values are presented as percent of controls (from Pezeshki *et al.* [157]).

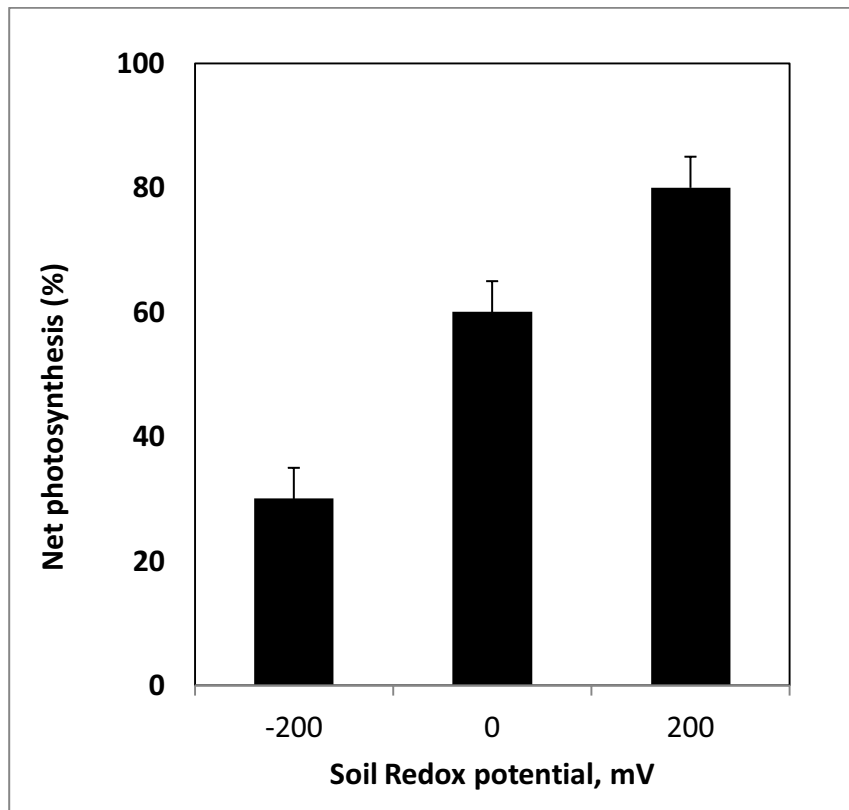


Figure 5. Response of light saturated leaf photosynthesis to root-zone redox potential (Eh) for 5-year-old (A) *Fraxinus pennsylvanica* and (B) *Quercus bicolor* in a created wetland (from Pennington and Walters [28]).

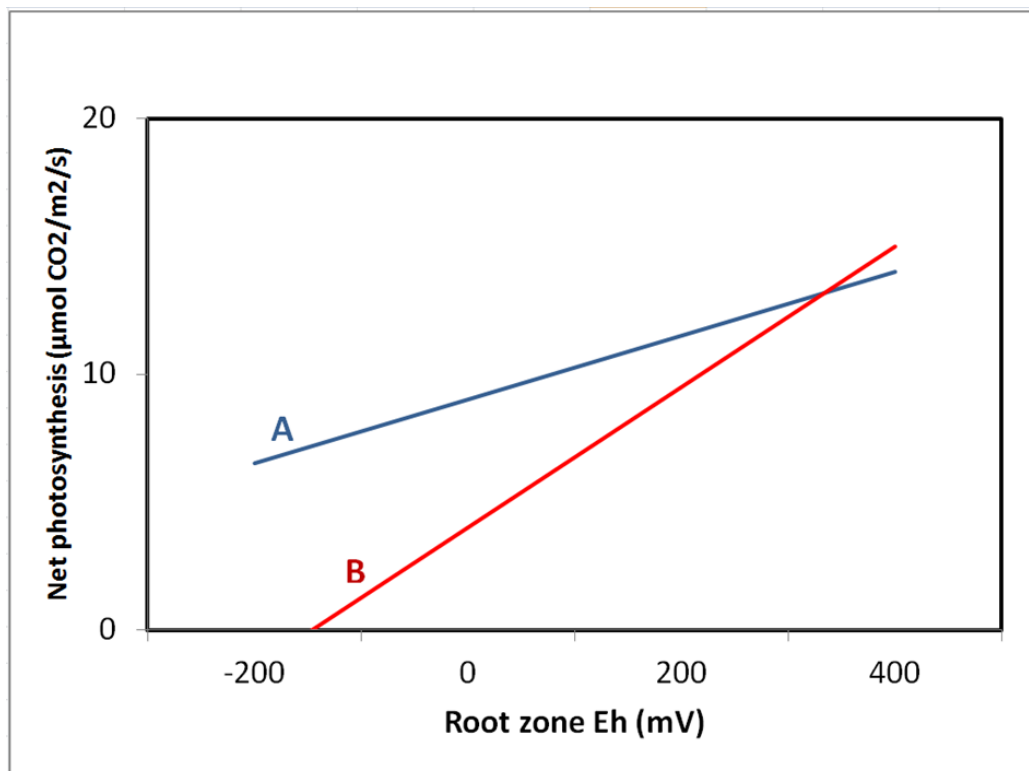


Figure 6. A generalized relationship between photosynthetic activity in wetland plants and soil redox potential (from Pezeshki [22,23]).

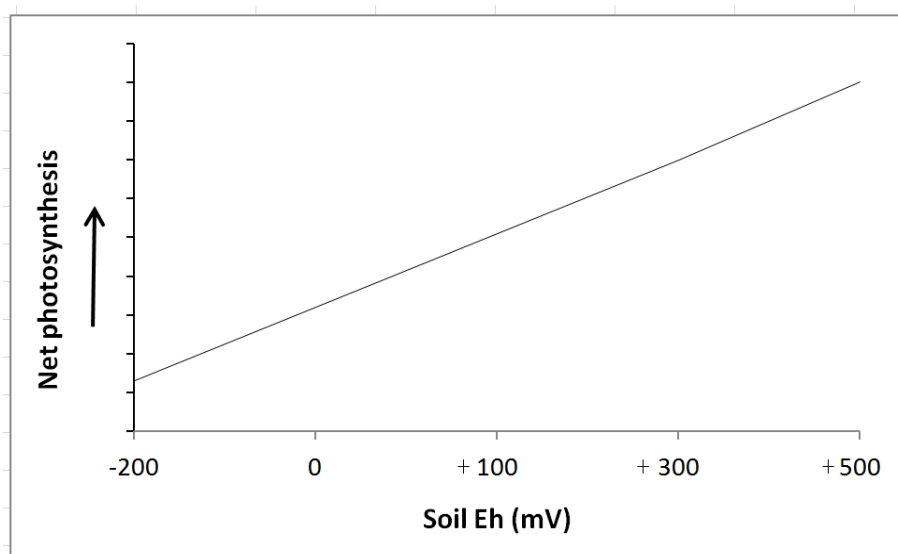


Table 1. Photosynthetic responses of selected marsh plants and wetland/bottomland woody species to the intensity of soil reduction. Values represent percent reduction in net photosynthetic rates compared to plants grown under oxidized ($E_h > +400$ mV) conditions or percent of pre-stress levels.

Species	Soil E_h (mV)	Photosyn. Response (%)	Reference
Marsh plants			
<i>Typha domingensis</i>	+200	18	[157]
	0	49	[157]
	−200	75	[157]
<i>Cladium Jamaicense</i>	+200	24	[157]
	0	46	[157]
	−200	100	[157]
<i>Spartina alterniflora</i>	<−200	15–21	[131]
<i>Spartina patens</i>	+230	7	[91]
	−110	18	[91]
Woody species			
<i>Quercus lyrata</i>	+340	54	[93]
	+175	66	[93]
<i>Ligustrum sinense</i>	+200/−200	86	[132]
<i>Taxodium distichum</i>	−70	5	[158]
	−160	22	[158]
<i>Taxodium distichum</i>	+350/+175	5	[159]
<i>Taxodium distichum</i>	−40/−70	36	[128]
	+18/+172	Decreased/recovered	[160]
<i>Salix nigra</i>	−130	53	[158]
	+50 to −80	5	[86]
<i>Quercus nuttallii</i>	+100/−220	35–68	[88]
<i>Quercus nuttallii</i>	+350/+175	21	[159]
<i>Quercus falcata</i>	+100/−220	65–87	[88]
<i>Quercus michauxii</i>	+350/+175	58	[159]

Chlorophyll fluorescence has been used to assess intact plants for detecting stress effects such as flooding effects [130] particularly the effects on PSII functioning. Utilizing this technique, Pociecha *et al.* [117] reported that in flooded *Vicia faba* L. plants, there was an apparent damage to photosynthetic apparatus as indicated by lower Fv/Fm compared to control plants. However, in wetland plants such as *Salix nigra*, Eh drop to the range of −50 to −100 mV did not have any significant effect on Fv/Fm [86]. This Eh range represents a moderately reduced soil conditions thus may explain the lack of PSII response in a wetland species such as *S. nigra*. Additional research is needed to assess PSII response to low soil Eh in wetland plants.

Photosynthetic recovery is reported for some wetland species despite the continuation of low soil Eh conditions provided that the soil is moderately reduced [88,127,131,132]. Soil Eh below +150 mV led to decreased net photosynthesis in *Alnus japonica* seedlings and the rate of recovery was correlated with the development of adventitious roots [81,82]. Even if a substantial recovery of photosynthetic rates occur, the impact of initial reduction and the delayed and/or slow recovery on plant survival and growth may be substantial due to the disruption of carbon fixation and decrease in photosynthate production [28,61,88,128,129].

What are the mechanisms through which the low soil Eh condition reduces leaf photosynthetic activity in many wetland plants? There are numerous factors that may be responsible for the decrease of net photosynthesis. For instance, ethylene accumulation has been implicated and the effects may be due to loss of photosynthetic capacity of mesophyll [133]. Low soil Eh conditions could lead to reductions of net photosynthesis due to decreased leaf water potential, reduced rubisco activity [66], disruption in photosynthate transport [61], alterations in source-sink relationship or reduced sink demand [23,33,134,135]. Other factors that may contribute to the reduction in photosynthetic capacity include low leaf chlorophyll content and/or leaf chlorophyll degeneration, and dysfunctioning of PSII. Recent reports showed that flooding led to limitations on the quantum efficiency of PSII in certain crop plants [116,136]. Leaf chlorophyll content decreases in some wetland plants that are subjected to reduced soil conditions [137].

Rubisco is an important enzyme in photosynthesis that catalyzes carboxylation yielding two molecules of 3-phosphoglycerate and oxygenation that produces one molecule of 3-phosphoglycerate and one molecule of 2-phosphoglycolate [138]. Because activity of this enzyme is critical for photosynthesis, flood-induced reductions of photosynthesis may be due, at least partially, to decreases in rubisco activity. In addition, the recovery of rubisco activity may contribute to the observed recovery of net photosynthesis in some wetland plants [22,66,127]. Indeed changes in rubisco (EC 4.1.1.39) activity may be an early signal contributing to the reduction of leaf photosynthesis in flooded plants as reported in the literature [66,139,140]. In some crop species, stress leads to reduced rubisco activity and enhanced rubisco degradation [65,141,142]. Li *et al.* [143] showed that decreased gene expression of oxygen evolving complex, large subunits of Rubisco and ferredoxin in response to flooding may have contributed to the observed photosynthetic reduction.

Low soil Eh conditions influences translocation of various photosynthetic products as reported for some [61,144,145]. The effects include low ATP production resulting from disruption of the oxidative phosphorylation [56,146,147], carbohydrate synthesis, transport, allocation, and utilization [78,148–150]. Carbohydrate allocation patterns and translocation rates appear to be critical for withstanding hypoxic condition [149–151]. However, the specifics of wetland plant responses remain to be evaluated.

10. Growth and Biomass Production

Decrease in survival and biomass accumulation in response to low soil Eh conditions is reported in certain wetland species. For example, while *T. distichum* remained relatively unaffected by Eh as low as -160 mV (Figure 7a–c), *Carya illinoensis* showed dramatic response at Eh around -70 mV (Kludze and DeLaune [13,14,23,61,86,87]). Significant changes are also reported in root to shoot ratio in some species as the effects of soil reduction are usually more drastic on root systems than shoots [86,114,152]. While a range of responses to low soil Eh conditions may occur in a given species, these changes, nevertheless, occur within the context of an overall reduction in biomass accumulation as reported for flooded plants of many species (Pezeshki [23] and the references cited therein). Root and shoot dry weights in *S. patens* decreased by 40% and 25% as soil Eh dropped from $+200$ mV to -300 mV, respectively. Results clearly indicated the influence of soil Eh intensity on growth of this dominant U.S. Gulf coast marsh species. It also was demonstrated that roots were more sensitive to Eh intensity than shoots (also data by Kludze and DeLaune [87]). In general, Eh reduction has pronounced effects on root elongation (Figure 8). Similar conclusions were drawn from a study on a flood-tolerant woody species *Taxodium distichum* [17]. Pezeshki and DeLaune [153] reported cessation of root growth in *S. patens* at soil Eh of -100 mV. In addition, Pezeshki *et al.* [90] noted smaller root system in *S. patens* under reducing soil conditions and concluded that such reduction in sink size, may in part, be responsible for a negative feed-back inhibition of photosynthesis thus, reduction in productivity of this species.

The increase in oxygen loss rates reported under reducing soil Eh [14,87] may explain the reductions in root growth of several wetland species under low soil Eh conditions. *Cladium jamaicense* and *Typha domingensis* produced significantly less biomass at Eh of -150 mV compared to plants grown at oxidized Eh of $+600$ mV [155]. Inhibitory effects of low soil Eh on photosynthesis and growth of woody species has also been reported by Pennington and Walters [28]. Root growth is an energy dependent process requiring oxygen, thus, under flooded conditions, root functioning is affected rapidly because molecular oxygen is required as an electron acceptor for oxidative phosphorylation [33,154]. Root elongation was inhibited in some bottomland woody species when soil Eh fell below $+350$ mV [152]. Interestingly, the $+350$ mV is the approximate Eh level that signifies the onset of oxygen disappearance from the soil system [7]. Root penetration depth was also adversely affected under low soil Eh treatment resulting in development of shallow root system different in architecture than those of plants growing in aerated (Eh $> +400$ mV) conditions [152,153]. The critical threshold Eh that inhibited root elongation differed among wetland species ranging from $+300$ mV to -200 mV [152,156].

Soil Eh capacity also influences wetland plant gas exchange and growth [13,14]. In the study, plants were grown under controlled Eh to examine the effect of Eh on CO_2 fixation. Soil redox capacity was imposed by application of different levels of extra energy source, by adding granular D-glucose to the growth medium, while maintaining Eh intensity at -200 mV. Increases in soil Eh capacity led to decreased photosynthesis, root growth, and biomass in *Oryza sativa* while enhanced root porosity and radial oxygen loss rate (Figure 9). Other studies demonstrated that plant carbon fixation, root, and shoot growth were significantly inhibited in *S. patens* under increasing soil reduction capacity. Root and shoot dry weights decreased by 70 and 37% in high reduction capacity conditions compared to control plants, respectively [14].

Figure 7. Biomass accumulation, root/weight ratio, and survival of two woody species *Taxodium distichum* and *Carya illinoensis* in response to changes in soil Eh conditions (from Pezeshki and Delaune [158]).

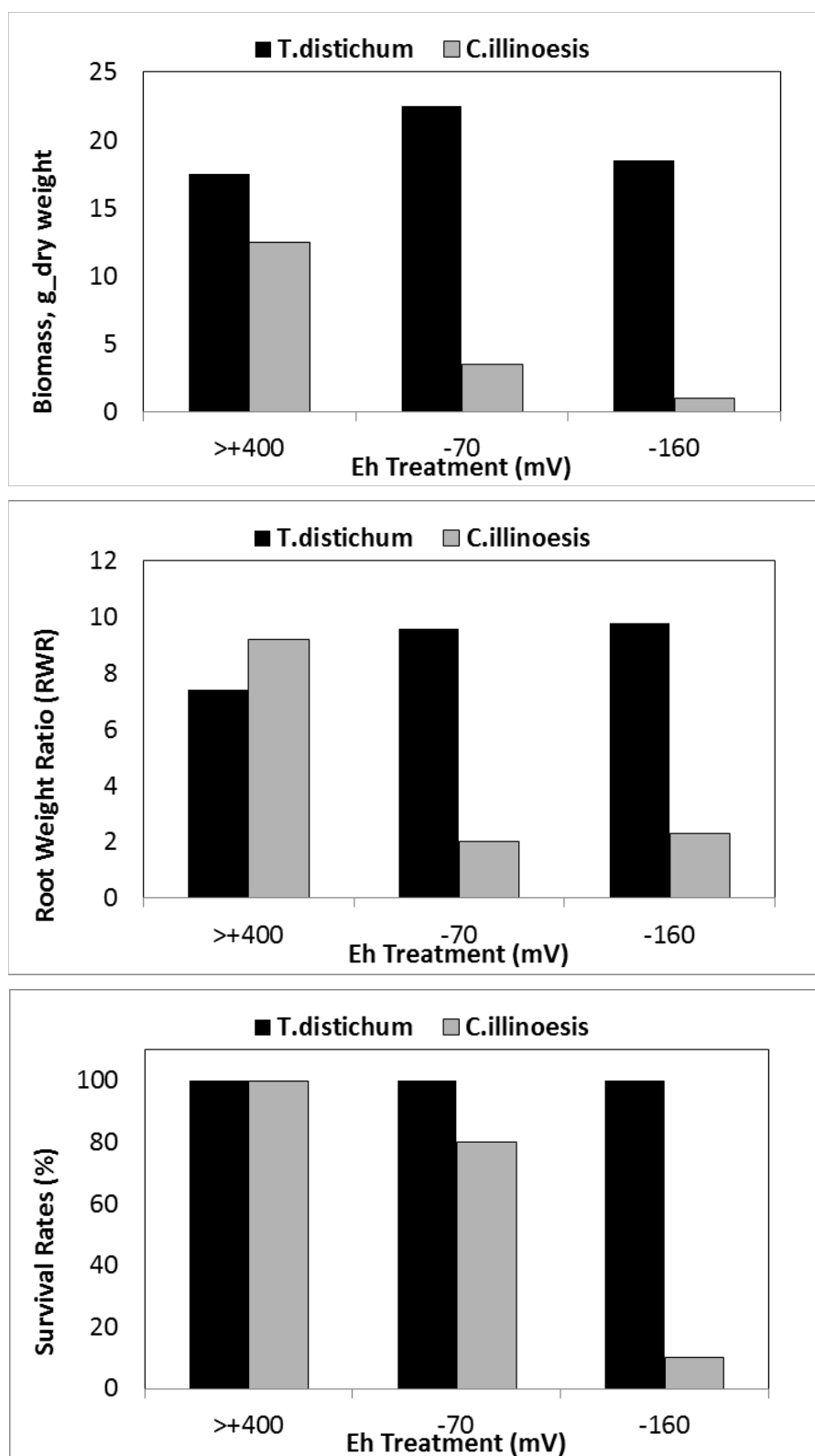


Figure 8. Responses of root elongation in *Spartina patens*, a brackish marsh species, to soil redox potential (Eh) (from Pezeshki and DeLaune [153]).

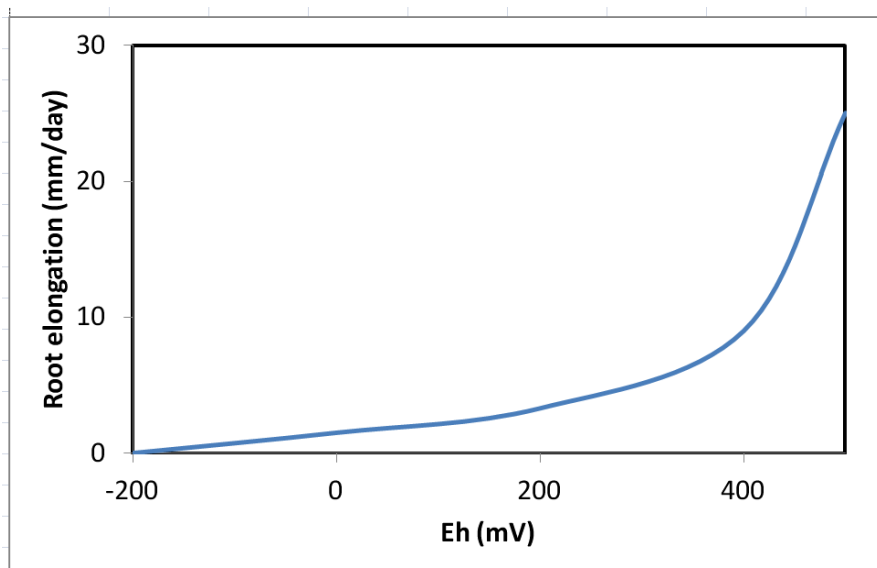
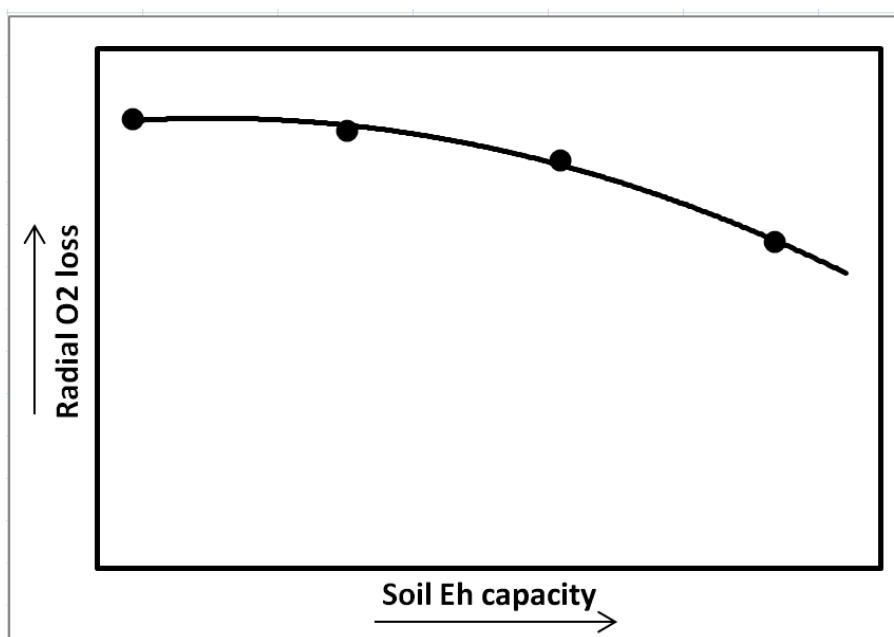


Figure 9. Radial O₂ loss (ROL) in *Spartina patens* in response to changes in soil reduction capacity while soil reduction intensity was maintained at −200 mV (Kludze and DeLaune [14]).



11. Concluding Remarks

There is a sufficient body of data to show that many plant functions are influenced by low soil Eh conditions. Wetland plant response is dependent on several factors including the species, duration of soil reduction, the timing, the intensity, and the capacity of soil reduction. The reducing condition of the soil is a major factor in wetland ecosystems that influences plant survival, growth, and productivity. Thus, quantifying soil reduction is critical to the understanding and interpretation of

wetland plant responses to such conditions. In addition, plant response to low soil Eh conditions also reflects species' ability to respond to such conditions by utilizing a variety of morphological, anatomical and metabolic defense mechanisms. Nevertheless, many wetland species including those that possess a wide range of tolerance/avoidance capabilities to cope with low soil redox conditions are impacted negatively. The impact is a reflection of the fact that reducing soil conditions encompass not only soil oxygen deprivation but also production of various compounds in the soil, many of which considered highly phytotoxic. Thus, soil reducing conditions exert substantial influence on critical plant processes including gas exchange, water relations, photosynthate partitioning, translocation, hormonal balance, nutrition, growth, and biomass production.

Based on the limited available data, both intensity and capacity of reduction appear to influence plant functioning in wetland ecosystems although the roles of both factors need further investigations. In wetland soils, plants are faced with a substantial demand for oxygen from roots and soil microbial populations, the potential for loss of oxygen to soil through root radial oxygen loss that could improve bulk soil Eh conditions but nevertheless may impose plant internal O₂ deficiency, and the adverse effects of soil phytotoxins that are by-products of soil reduction. The severity of oxygen loss and the effects of reduction intensity and capacity on plant functioning are clearly common but vary across species. The need for additional data on various aspects of plant functioning and growth in wetland ecosystems in response to soil redox conditions, in terms of the intensity and the capacity, as well as the specific effects of soil phytotoxins is clear.

References

1. Gambrell, R.P.; Patrick, W.H. Chemical and Microbiological Properties of Anaerobic Soils and Sediments. In *Plant Life in Anaerobic Environments*; Hook, D.D., Crawford, R.M.M., Eds.; Ann Arbor Science: Ann Arbor, MI, USA, 1978; pp. 375–423.
2. Ponnamperna, F.N. Effects of Flooding on Soils. In *Flooding and Plant Growth*; Kozlowski, T.T., Ed.; Academic Press Inc.: Orlando, FL, USA, 1984; pp. 1–44.
3. Gambrell, R.P.; DeLaune, R.D.; Patrick, W.H. Redox Processes in Soils Following Oxygen Depletion. In *Plant Life Under Oxygen Deprivation: Ecology, Physiology, and Biochemistry*; Jackson, M.B., Davies, D.D., Lambers, H., Eds.; SPB Academic Publishing BV: The Hague, The Netherlands, 1991; pp. 101–117.
4. Jackson, M.B.; Drew, M.C. Effects of Flooding on Growth and Metabolism of Herbaceous Plants. In *Flooding and Plant Growth*; Kozlowski, T.T., Ed.; Academic Press, Inc: Waltham, MA, USA, 1984; pp. 47–128.
5. Greenway, H.; Armstrong, W.; Colmer, T.D. Conditions leading to high CO₂ (>5 kPa) in waterlogged flooded soils and possible effects on root growth and metabolism. *Ann. Bot.* **2006**, *98*, 9–32.
6. Ponnamperna, F.N. The chemistry of submerged soil. *Adv. Agron.* **1972**, *24*, 29–96.
7. DeLaune, R.D.; Pezeshki, S.R.; Pardue, J.H. An oxidation-reduction buffer for evaluating physiological response of plants to root oxygen stress. *Environ. Exp. Bot.* **1990**, *30*, 243–247.
8. Patrick, W.H.; DeLaune, R.D. Chemical and biological redox systems affecting nutrient availability in the coastal wetlands. *Geosci. Man* **1977**, *XVIII*, 131–137.

9. Reddy, K.R.; DeLaune, R.D. *Biogeochemistry of Wetlands: Science and Applications*; CRC Press: Boca Raton, FL, USA, 2008; p. 774.
10. Pearsall, W.H.; Mortimer, C.H. Oxidation-reduction potentials in waterlogged soils, natural waters and muds. *J. Ecol.* **1939**, *27*, 483–501.
11. Mortimer, C.H. The exchange of dissolved substances between mud and water in lakes. *J. Ecol.* **1941**, *29*, 280–329.
12. Mitsch, W.J.; Gosselink, J.G. *Wetlands*, 4th ed.; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2007; p. 582.
13. Kludze, H.K.; DeLaune, R.D. Straw application effects on Methane and oxygen exchange and growth in rice. *Soil Sci. Soc. Am. J.* **1995**, *59*, 824–830.
14. Kludze, H.K.; DeLaune, R.D. Gaseous exchange and wetland plant response to soil redox intensity and capacity. *Soil Sci. Soc. Am. J.* **1995**, *59*, 939–945.
15. Kludze, H.K. Gaseous exchange and wetland plant response to soil redox conditions. Ph.D. Dissertation, Louisiana State University, Baton Rouge, LA, USA, 1994.
16. Kludze, H.K.; DeLaune, R.D.; Patrick, W.H. Aerenchyma formation and methane and oxygen exchange in rice. *Soil. Sci. Soc. Am. J.* **1993**, *51*, 386–391.
17. Kludze, H.K.; Pezeshki, S.R.; DeLaune, R.D. Evaluation of root oxygenation and growth in baldcypress in response to short-term soil hypoxia. *Can. J. For. Res.* **1994**, *24*, 804–809.
18. Sorrell, B.K.; Brix, H.; Orr, P.T. Oxygen exchange by entire root system of *Cyperus involucratus* and *Eleocharis sphacelata*. *J. Aquat. Plant Manage.* **1993**, *31*, 24–28.
19. Armstrong, W.; Brandle, R.; Jackson, M.B. Mechanisms of flood tolerance in plants. *Acta Bot. Neerl.* **1994**, *43*, 307–358.
20. Armstrong, J.; Armstrong, W.; Beckett, P.M.; Halder, J.E.; Lythe, S.; Holt, R.; Sinclair, A. Pathways of aeration and the mechanisms and beneficial effects of humidity- and venturi-induced convections in *Phragmites australis*. *Aquat. Bot.* **1996**, *54*, 177–197.
21. Armstrong, J.; Armstrong, W.; van Der Putten, W.H. *Phragmites* die-back: Bud and root death, blockage within the aeration and vascular systems and the possible role of phytotoxins. *New Phytol.* **1996**, *133*, 399–414.
22. Pezeshki, S.R. Plant Responses to Flooding. In *Plant-Environment Interactions*; Wilkinson, R.E., Ed.; Marcel Dekker, Inc.: New York, NY, USA, 1994; pp. 289–321.
23. Pezeshki, S.R. Wetland plant responses to flooding. *Environ. Exp. Bot.* **2001**, *46*, 299–312.
24. Sorrell, B.K. Effect of external oxygen demand on radial oxygen loss by *Juncus* roots in titanium citrate solutions. *Plant Cell Environ.* **1999**, *22*, 1587–1593.
25. Van Wijck, C.; de Groot, C.J.; Grillas, P. The effect of anaerobic sediment on the growth of *Potamogeton pectinatus*: The role of organic matter, sulphide, and ferrous iron. *Aquat. Bot.* **1992**, *44*, 31–49.
26. Laskov, C.; Horn, O.; Hupfer, M. Environmental factors regulating the radial oxygen loss from roots of *Myriophyllum spicatum* and *Potamogeton crispus*. *Aquat. Bot.* **2006**, *84*, 333–340.
27. Armstrong, W.; Wright, E.J.; Lythe, S.; Gaynard, T.J. Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a humer salt marsh. *J. Ecol.* **1985**, *73*, 323–339.
28. Pennington, M.R.; Walters, M.B. The response of vegetation zonation and soil redox potential in created wetlands. *For. Ecol. Manag.* **2006**, *233*, 1–10.

29. Davy, A.J.; Brown, M.J.H.; Mossman, H.L.; Grant, A. Colonization of a newly developing saltmarsh: Disentangling independent effects of elevation and redox potential on halophytes. *J. Ecol.* **2001**, *99*, 1350–1357.
30. Justin, S.H.F.W.; Armstrong, W. The anatomical characteristics of roots and plant response to soil flooding. *New Phytol.* **1987**, *106*, 465–495.
31. Pedersen, O.; Sand-Jensen, K. Adaptation of submerged *Lobelia dortmanna* to aerial life form: Morphology, carbon sources, and oxygen dynamics. *Oikos* **1992**, *65*, 89–96.
32. Pedersen, O.; Sand-Jensen, K.; Revsbech, N.P. Diel pulses of O₂ and CO₂ in sandy lake sediments inhabited by *Lobelia dortmanna*. *Ecology* **1995**, *76*, 1536–1545.
33. Drew, M.C. Sensing soil oxygen. *Plant Cell Environ.* **1990**, *13*, 681–693.
34. Drew, M.C. Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. *Ann. Rev. Plant Physiol. Plant Mol. Biol.* **1997**, *48*, 223–250.
35. Hook, D.D.; Crawford, R.M.M. *Plant Life in Anaerobic Environments*; Ann Arbor Science: Woburn, MA, USA, 1978; p. 564.
36. Vartapetian, B.B.; Jackson, M.B. Plant adaptations to anaerobic stress. *Ann. Bot.* **1997**, *79*, 3–20.
37. Armstrong, W. The relationship between oxidation-reduction potentials and oxygen diffusion levels in some waterlogged organic soils. *J. Soil Sci.* **1967**, *18*, 27–34.
38. Turner, F.T.; Patrick, W.H. Chemical changes in waterlogged soils as a result of oxygen depletion. *Trans. 9th Int. Congr. Soil Sci.* **1968**, *4*, 53–56.
39. Armstrong, W.; Armstrong, J.; Beckett, P.M. Pressurized aeration in wetland macrophytes: Some theoretical aspects of humidity-induced convection and thermal transpiration. *Folia Geobot. Phytotax.* **1996**, *31*, 25–36.
40. Greenway, H.; Gibbs, J. Mechanisms of anoxia tolerance in plants: II> Energy requirements for maintenance and energy distribution to essential processes. *Funct. Plant Biol.* **2003**, *30*, 999–1036.
41. Voesenek, L.A.C.J.; Colmer, T.D.; Pierik, R.; Millenaar, F.F.; Peeters, A.J.M. How plants cope with submergence. *New Phytol.* **2006**, *170*, 213–226.
42. DeLaune, R.D.; Smith, C.J.; Patrick, W.H. Nitrogen losses from a Louisiana Gulf Coast salt marsh. *Est. Coast. Shelf Sci.* **1983**, *17*, 133–141.
43. Armstrong, J.; Drew, M.C. Root Growth and Metabolism under Oxygen Deficiency. In *Plant Roots: The Hidden Half*; Waisel, Y., Eshel, A., Kafkaf, U., Eds.; Marcel Dekker: New York, NY, USA, 2002; pp. 729–761.
44. DeLaune, R.D.; Patrick, W.H.; Buresh, R.J. Sedimentation rates determined by Cs-137 dating in a rapidly accreting salt marsh. *Nature* **1978**, *275*, 532–533.
45. Drew, M.C.; Lynch, J.M. Soil anaerobiosis, micro-organisms and root functions. *Ann. Rev. Phytopathol.* **1980**, *18*, 37–66.
46. King, G.M.; Klug, M.J.; Wiegert, R.G.; Chalmers, A.G. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia saltmarsh. *Science* **1982**, *218*, 61–63.
47. Ingold, A.; Havill, D.C. The influence of sulfide on the distribution of higher plants in salt marshes. *J. Ecol.* **1984**, *72*, 1043–1054.
48. Havill, D.C.; Ingold, A.; Pearson, J. Sulfide tolerance in coastal halophytes. *Vegetatio* **1985**, *62*, 279–285.

49. Tanaka, A.; Mulleriyawa, R.P.; Yasu, T. Possibility of hydrogen sulfide induced iron toxicity of the rice plant. *Soil Sci. Plant Nutr.* **1968**, *4*, 1–6.
50. Allam, A.I.; Hollis, J.P. Sulfide inhibition of oxidases in rice roots. *Phytopathology* **1972**, *62*, 634–639.
51. Rao, D.N.; Mikkelsen, D.S. Effects of acidic, propionic, and butyric acids on rice seedling growth and nutrition. *Plant Soil* **1977**, *47*, 323–334.
52. Armstrong, J.; Armstrong, W. *Phragmites* dieback: Toxic effects of propionic, butyric and caproic acids in relation to pH. *New Phytol.* **1999**, *142*, 201–217.
53. Atwell, B.J.; Greenway, H. The relationship between growth and oxygen uptake in hypoxic rice seedlings. *J. Exp. Bot.* **1987**, *38*, 454–465.
54. Armstrong, W. Aeration in higher plants. *Adv. Bot. Res.* **1979**, *7*, 225–332.
55. Drew, M.C. Soil aeration and plant root metabolism. *Soil Sci.* **1992**, *154*, 259–268.
56. Hopkins, W.G.; Huner, N.P. *Introduction to Plant Physiology*, 4th ed.; John Wiley & Sons, Inc.: New York, NY, USA, 2009; p. 503.
57. Keeley, J.E. Population differentiation along a flood frequency gradient: Physiological adaptation to flooding in *Nyssa sylvatica*. *Ecol. Monogr.* **1979**, *49*, 89–108.
58. Mendelssohn, I.A.; McKee, K.L.; Patrick, W.H. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. *Science* **1981**, *214*, 439–441.
59. Crawford, R.M.M. Oxygen availability as an ecological limit to plant distribution. *Adv. Ecol. Res.* **1992**, *23*, 93–285.
60. Kennedy, R.A.; Rumpho, M.E.; Fox, T.C. Aerobic metabolism in plants. *Plant Phys.* **1992**, *100*, 1–6.
61. Kogawara, S.; Yamanoshita, T.; Norisada, M.; Masumori, M.; Kojima, K. Photosynthesis and photoassimilate transport during root hypoxia in *Melaleuca cajuputi*, a flood-tolerant species, and in *Eucalyptus camadulensis*, a moderately flood-tolerant species. *Tree Physiol.* **2006**, *26*, 1413–1423.
62. Roberts, J.K.M.; Andrade, F.H.; Anderson, J.C. Further evidence that cytoplasmic acidosis is a determinant of flooding intolerance in plants. *Plant Physiol.* **1985**, *77*, 492–494.
63. Barmore, C.R. Effect of ethylene on chlorophyllase activity and chlorophyll content in calamond in rind tissue. *HortScience* **1975**, *10*, 595–596.
64. Berry, J.; Bjorkman, O. Photosynthetic and adaptation to temperature in higher plants. *Annu. Rev. Plant Physiol.* **1980**, *31*, 491–543.
65. Majumdar, S.; Ghosh, S.; Glick, B.R.; Dumbroff, E.B. Activities of chlorophyllase, phosphoenolpyruvate carboxylase and ribulose-1, 5-bisphosphate carboxylase in the primary leaves of soybean during senescence and drought. *Physiol. Plant* **1991**, *81*, 473–480.
66. Pezeshki, S.R. Response of baldcypress seedlings to hypoxia: Leaf protein content, ribulose-1, 5-bisphosphate carboxylase/oxygenase activity and photosynthesis. *Photosynthetica* **1994**, *30*, 59–68.
67. Li, S.; Pezeshki, S.R.; Goodwin, S.; Shields, F.D. Physiological responses of black willow (*Salix nigra*) cuttings to a range of soil moisture regimes. *Photosynthetica* **2004**, *42*, 585–590.
68. Saglio, P.H.; Drew, M.C.; Pradet, A. Metabolic acclimation to anoxia induced by low (2–4 KPa partial pressure) oxygen pretreatment (hypoxia) in root tips of *Zea mays*. *Plant Physiol.* **1988**, *86*, 61–66.

69. Bertani, A.; Brambilla, I.; Menegus, F. Effect of anaerobiosis on rice seedlings: Growth, metabolic rate and fate of fermentation products. *J. Exp. Bot.* **1980**, *31*, 325–331.
70. MacDonald, R.C.; Kimmerer, T.W. Metabolism of transpired ethanol by eastern cottonwood (*Populus deltoides*). *Plant Physiol.* **1993**, *102*, 173–179.
71. Jackson, M.B. Long-distance signaling from roots to shoots assessed: The flooding story. *J. Exp. Bot.* **2002**, *53*, 175–181.
72. Dat, J.F.; Capelli, N.; Folzer, H.; Bourgeade, P.; Badot, P.-M. Sensing and signaling during plant flooding. *Plant Physiol. Biochem.* **2004**, *42*, 273–282.
73. Hattori, Y.; Nagai, K.; Furukawa, S.; Song, X.; Kawano, R.; Sakakibara, H.; Wu, J.; Matsumoto, T.; Yoshimura, A.; Kitano, H.; *et al.* The ethylene response factors SNORKEL1 and SNORKEL2 allow rice to adapt to deep water. *Nature* **2009**, *460*, 1026–1030.
74. McKee, K.L. Growth and physiological responses of neotropical mangrove seedlings to root zone hypoxia. *Tree Physiol.* **1996**, *16*, 883–889.
75. Youssef, T.; Saenger, P. Anatomical adaptive strategies to flooding and rhizosphere oxidation in mangrove seedlings. *Aust. J. Bot.* **1996**, *44*, 297–313.
76. Youssef, T.; Saenger, P. Photosynthetic gas exchange and accumulation of phytotoxins in mangrove seedlings in response to soil physico-chemical characteristics associated with waterlogging. *Tree Physiol.* **1998**, *18*, 317–324.
77. Teal, J.M.; Kanwisher, J.W. Gas transport in the marsh grass *Spartina alterniflora*. *J. Exp. Bot.* **1966**, *17*, 355–361.
78. Kozłowski, T.T. Responses of woody plants to flooding and salinity. *Tree Physiol. Monogr.* **1997**, *1*, 1–29.
79. Armstrong, W.; Justin, S.H.F.W.; Beckett, P.M.; Lythe, S. Root adaptation to soil waterlogging. *Aquat. Bot.* **1991**, *39*, 57–73.
80. Perata, P.; Alpi, A. Plant responses to anaerobiosis. *Plant Sci.* **1993**, *93*, 1–17.
81. Iwanaga, F.; Yamamoto, F. Growth, morphology and photosynthetic activity in flooded *Alnus japonica* seedlings. *J. For. Res.* **2007**, *12*, 243–246.
82. Iwanaga, F.; Yamamoto, F. Effects of flooding depth on growth, morphology and photosynthesis in *Alnus japonica* species. *New For.* **2008**, *35*, 1–14.
83. Dacey, J.W.H. Pressurized ventilation in the yellow water lily. *Ecology* **1981**, *62*, 1137–1147.
84. Armstrong, W.; Beckett, P.M. Internal aeration and the development of stelar anoxia in submerged roots: A multi-shelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers, and the rhizosphere. *New Phytol.* **1987**, *105*, 221–245.
85. Luxmoore, R.J.; Sojka, R.E.; Stolzy, L.H. Root porosity and growth responses of wheat to aeration and light intensity. *Soil Sci.* **1972**, *113*, 354–357.
86. Li, S.; Pezeshki, S.R.; Shields, F.D. Partial flooding enhances aeration in adventitious roots of black willow (*Salix nigra*) cuttings. *J. Plant Physiol.* **2006**, *163*, 619–628.
87. Kludze, H.K.; DeLaune, R.D. Methane emission and growth of *Spartina patens* in response to soil redox intensity. *Soil Sci. Soc. Am. J.* **1994**, *58*, 1838–1845.
88. Pezeshki, S.R.; Anderson, P.A. Responses of three bottomland woody species with different flood-tolerance capabilities to various flooding regimes. *Wetl. Ecol. Manag.* **1997**, *4*, 245–256.

89. Brix, H.; Sorrell, B.K. Oxygen stress in wetland plants: Comparison of de-oxygenated and reducing root environments. *Funct. Ecol.* **1996**, *10*, 521–526.
90. Pezeshki, S.R.; Matthews, S.W.; DeLaune, R.D. Root cortex structure and metabolic response of *Spartina patens* to soil redox conditions. *Environ. Exp. Bot.* **1991**, *31*, 91–97.
91. Pezeshki, S.R.; Pardue, J.H.; DeLaune, R.D. The influence of oxygen deficiency and redox potential on alcohol dehydrogenase activity, root porosity, ethylene production and photosynthesis in *Spartina patens*. *Environ. Exp. Bot.* **1993**, *33*, 565–573.
92. Pezeshki, S.R.; DeLaune, R.D.; Anderson, P.H. Effect of flooding on elemental uptake and biomass allocation in seedlings of three bottomland tree species. *J. Plant Nutr.* **1999**, *22*, 1481–1494.
93. DeLaune, R.D.; Pezeshki, S.R.; Lindau, C.W. Influence of soil redox potential on nitrogen uptake and growth of wetland oak seedlings. *J. Plant Nutr.* **1998**, *21*, 757–768.
94. DeLaune, R.D.; Jugsujinda, A.; Reddy, K.R. Effect of root oxygen stress on phosphorus uptake by cattail. *J. Plant Nutr.* **1999**, *22*, 459–466.
95. Else, M.; Coupland, A.D.; Dutton, L.; Jackson, M.B. Decreased root hydraulic conductivity reduces leaf water potential, initiates stomatal closure, and slows leaf expansion in flooded plants of castor oil (*Ricinus communis*) despite diminished delivery of ABA from roots to shoots in xylem sap. *Physiol. Plant* **2001**, *111*, 46–54.
96. Jackson, M.B.; Saker, L.R.; Crisp, C.M.; Else, M.A.; Janowiak, F. Ionic and pH signaling from roots to shoots of flooded tomato plants in relation to stomatal closure. *Plant Soil* **2003**, *253*, 103–113.
97. Gibbs, J.; Turner, D.W.; Armstrong, W.; Darwent, M.J.; Greenway, H. Response to oxygen deficiency in primary maize roots. I. Development of oxygen deficiency in the stele reduces radial solute transport to the xylem. *Aust. J. Plant Physiol.* **1998**, *25*, 745–758.
98. Hook, D.D.; DeBell, D.S.; McKee, W.H.; Askew, J.L. Responses of loblolly pine (mesophyte) and swamp tupelo (hydrophyte) seedlings to soil flooding and phosphorous. *Plant Soil* **1983**, *71*, 387–394.
99. Pezeshki, S.R.; Pan, S.Z.; DeLaune, R.D.; Patrick, W.H. Sulfide-induced toxicity: Inhibition of carbon assimilation in *Spartina alterniflora*. *Photosynthetica* **1988**, *22*, 437–442.
100. Pavanadasivam, V.; Axley, J.H. Influence of flooding on the availability of soil zinc. *Commun. Soil Sci. Plant Anal.* **1980**, *11*, 163–174.
101. Good, B.G.; Patrick, W.H. Gas composition and respiration of water oak (*Quercus nigra*) and green ash (*Fraxinus pennsylvanica*) roots after prolonged flooding. *Plant Soil* **1987**, *97*, 419–427.
102. McKevlin, M.R.; Hook, D.D.; McKee, W.H.; Wallace, S.U.; Woodruff, J.R. Loblolly pine seedling root anatomy and iron accumulation as affected by soil waterlogging. *Can. J. For. Res.* **1987**, *17*, 1257–1264.
103. Gries, C.; Kappen, L.; Losch, R. Mechanism of flood tolerance in reed (*Phragmites australis*). *New Phytol.* **1990**, *114*, 589–593.
104. Armstrong, W. Waterlogged Soils. In *Environment and Plant Ecology*; Etherington, J.R., Ed.; Wiley: New York, NY, USA, 1975; p. 181.
105. Carlson, P.R.; Forrester, J. Uptake of dissolved sulfide by *Spartina alterniflora*: Evidence from natural sulfur isotope abundance ratios. *Science* **1982**, *216*, 633–635.

106. Pearson, J.; Havill, D.C. The effect of hypoxia and sulfide on culture grown wetland and non-wetland plants. *J. Exp. Bot.* **1988**, *39*, 363–370.
107. Pezeshki, S.R.; DeLaune, R.D.; Pan, S.Z. Relationship of soil hydrogen sulfide level to net carbon assimilation of *Panicum hemitomon* and *Spartina patens*. *Vegetatio* **1991**, *95*, 159–166.
108. Shimazaki, K.; Sugahara, K. Inhibition site of the electron transport system in lettuce chloroplasts by fumigation of leaves with SO₂. *Plant Cell Physiol.* **1980**, *21*, 125–135.
109. Wellburn, A.R.; Higginson, C.; Robinson, D.; Walmsley, C. Biochemical explanations of more than additive inhibitory effects of low atmospheric levels of sulphur dioxide plus nitrogen dioxide upon plants. *New Phytol.* **1981**, *88*, 223–237.
110. Garsed, S.G. The use of sulfite solution for studying the effects of SO₂ on higher plants. *Environ. Pollut. Ser.* **1981**, *24*, 883–886.
111. Khan, A.A.; Malhotra, S.S. Ribulose biphosphate carboxylase and glycollate oxidase from jack pine: Effects of sulphur dioxide fumigation. *Phytochemistry* **1982**, *21*, 2607–2612.
112. Dropff, M.J. Physiological effects of sulfide dioxide: 1. The effect of SO₂ on photosynthesis and stomatal regulation of *Vicia faba* L. *Plant Cell Environ.* **1987**, *10*, 753–760.
113. Furtig, K.; Ruegsegger, A.; Brunhold, C.; Brandle, R. Sulfide utilization and injuries in hypoxic roots and rhizomes of Common Reed (*Phragmites australis*). *Folia Geobot. Phytotax.* **1996**, *31*, 143–151.
114. DeLaune, R.D.; Smith, C.J.; Patrick, W.H. Relationship of marsh elevation, redox potential and sulfide to *Spartina alterniflora* productivity. *Soil Sci. Soc. Am. J.* **1983**, *47*, 930–935.
115. Everard, J.D.; Drew, M.C. Mechanisms controlling changes in water movement through the roots of *Helianthus annuus* L. during continuous exposure to oxygen deficiency. *J. Exp. Bot.* **1989**, *40*, 95–103.
116. Else, M.A.; Janowiak, F.; Atkinson, C.J.; Jackson, M.B. Root signals and stomatal closure in relation to photosynthesis, chlorophyll a fluorescence and adventitious rooting of flooded tomato plants. *Ann. Bot.* **2009**, *103*, 313–323.
117. Pocięcha, E.; Koscielniak, J.; Filek, W. Effects of root flooding and stage of development on the growth and photosynthesis of field bean (*Vicia faba* L. *minor*). *Acta Physiol. Plant.* **2008**, *30*, 529–535.
118. Naumann, J.C.; Young, D.R.; Anderson, J.E. Leaf chlorophyll fluorescence and physiological response to freshwater and saltwater flooding in the evergreen shrub, *Myrica cerifera*. *Environ. Exp. Bot.* **2008**, *63*, 402–409.
119. Hiron, R.W.P.; Wright, S.T.C. The role of endogenous abscisic acid in the response of plants to stress. *J. Exp. Bot.* **1973**, *24*, 769–781.
120. Pereira, J.S.; Kozłowski, T.T. Variation among woody angiosperms in response to flooding. *Physiol. Plant.* **1977**, *41*, 184–192.
121. Sena Gomes, A.R.; Kozłowski, T.T. Responses of *Melaleuca quinquenervia* seedlings to flooding. *Physiol. Plant* **1980**, *49*, 373–377.
122. Tang, Z.C.; Kozłowski, T.T. Some physiological and morphological responses of *Quercus macrocarpa* seedlings to flooding. *Can. J. For. Res.* **1982**, *12*, 196–202.
123. Pezeshki, S.R.; Chambers, J.L. Stomatal and photosynthetic response of sweetgum (*Liquidambar styraciflua* L.) to flooding. *Can. J. For. Res.* **1985**, *15*, 371–375.

124. Pezeshki, S.R.; Chambers, J.L. Response of cherrybark oak (*Quercus falcata* var. *pagodaefolia*) seedlings to short-term flooding. *For. Sci.* **1985**, *31*, 760–771.
125. Pezeshki, S.R.; DeLaune, R.D.; Patrick, W.H. Differential Response of selected mangroves to soil flooding and salinity: Gas exchange and biomass partitioning. *Can. J. For. Res.* **1990**, *20*, 869–874.
126. Pezeshki, S.R.; DeLaune, R.D.; Meeder, J.F. Carbon assimilation and biomass partitioning in *Avicennia germinans* and *Rhizophora mangle* seedlings in response to soil redox conditions. *Environ. Exp. Bot.* **1997**, *37*, 161–171.
127. Pezeshki, S.R. Differences in patterns of photosynthetic responses to hypoxia in flood-tolerant and flood-sensitive tree species. *Photosynthetica* **1993**, *28*, 423–430.
128. Krauss, K.W.; Doyle, T.W.; Howard, R.J. Is there evidence of adaptation to tidal flooding in saplings of baldcypress subjected to different salinity regimes? *Environ. Exp. Bot.* **2009**, *67*, 118–126.
129. Gravatt, D.A.; Kirby, C.J. Patterns of photosynthesis and starch allocation in seedlings of four bottomland hardwood tree species subjected to flooding. *Tree Physiol.* **1998**, *18*, 411–417.
130. Mielke, M.S.; Shaffer, B. Leaf gas exchange, chlorophyll fluorescence and pigment indexes of *Eugenia uniflora* L. in response to changes in light intensity and soil flooding. *Tree Physiol.* **2010**, *30*, 45–55.
131. Pezeshki, S.R.; DeLaune, R.D.; Patrick, W.H. Effect of fluctuating rhizosphere redox potential on carbon assimilation of *Spartina alterniflora*. *Oecologia* **1989**, *80*, 132–135.
132. Brown, C.E.; Pezeshki, S.R. A study on waterlogging as a potential silvicultural tool to control *Ligustrum sinense* populations in western Tennessee. *Wetlands* **2000**, *20*, 429–437.
133. Taylor, G.E.; Gunderson, C.A. Physiological site of ethylene effects on carbon dioxide assimilation in *Glycine max*. *Plant Physiol.* **1988**, *86*, 85–92.
134. Wample, R.L.; Thornton, R.K. Differences in the response of sunflower (*Helianthus annuus*) subjected to flooding and drought stress. *Physiol. Plant* **1984**, *61*, 611–616.
135. Pezeshki, S.R.; Santos, M.I. Relationship among rhizosphere oxygen deficiency, root restriction, photosynthesis and growth in baldcypress (*Taxodium distichum*) seedlings. *Photosynthetica* **1998**, *35*, 381–390.
136. Ahmed, S.; Nawata, E.; Sakuratania, T. Changes of endogenous ABA and ACC and their correlation to photosynthesis and water relations in mugbean (*Vigna radiate*) during waterlogging. *Environ. Exp. Bot.* **2006**, *57*, 278–284.
137. McKevlin, M.R.; Hook, D.D.; McKee, W.H. Growth and nutrient use efficiency of water tupelo seedlings in flooded and well drained soil. *Tree Physiol.* **1995**, *15*, 753–758.
138. Bowes, G. Growth at elevated CO₂: Photosynthetic responses mediated through rubisco. *Plant Cell Environ.* **1991**, *14*, 795–806.
139. Vu, J.C.V.; Yelenosky, G. Photosynthetic responses of rough lemon and sour orange to soil flooding, chilling and short-term temperature fluctuation during growth. *Environ. Exp. Bot.* **1992**, *32*, 471–477.
140. Liao, C.T.; Lin, C.H. Effect of flooding stress on photosynthetic activities of *Momordica charantia*. *Plant Physiol. Biochem.* **1994**, *32*, 479–485.

141. Dann, M.S.; Pell, E.J. Decline of activity and quantity of ribulose biphosphate carboxylase/owxygenase and net photosynthesis in ozone-treated potato foliage. *Plant Physiol.* **1989**, *91*, 427–432.
142. Lauer, M.J.; Pallardy, S.G.; Belvins, D.C.; Randall, D.D. Whole leaf carbon exchange characteristics of phosphate deficient soybeans (*Glycine max L.*). *Plant Physiol.* **1989**, *91*, 848–854.
143. Li, S.; Goodwin, S.; Pezeshki, S.R. Photosynthetic gene expression in black willow under various soil moisture regimes. *Biol. Plant* **2007**, *51*, 593–596.
144. Sij, J.W.; Swanson, C.A. Effect of petiole anoxia on phloem transport in squash. *Plant Physiol.* **1973**, *51*, 368–371.
145. Qureshi, F.A.; Spanner, D.C. The effect of nitrogen on the movement of tracers down the stolon of *Saxifraga sarmentosa* with some observations on the influence of light. *Planta* **1973**, *110*, 131–144.
146. Vartapetian, B.B. Flood-Sensitive Plants under Primary and Secondary Anoxia: Ultrastructural and Metabolic Responses. In *Plant Life Under Oxygen Deprivation*; Jackson, M.B., Davies, D.D., Lambers, H., Eds.; SPB Academic Publishing: The Hague, The Netherlands, 1991; pp. 201–216.
147. Kennedy, R.A.; Fox, T.C.; Everard, J.D.; Rumpho, M.E. Biochemical Adaptations to Anoxia: Potential Role of Mitochondrial Metabolism to Flood Tolerance in *Echinochloa Phyllopogon* (Barnyard Grass). In *Plant Life Under Oxygen Deprivation*; Jackson, M.B., Davies, D.D., Lambers, H., Eds.; SPB Academic Publishing: The Hague, The Netherlands, 1991; pp. 217–227.
148. Yamamoto, F.; Kozlowski, T.T. Effect of flooding, tilting of stem, and ethrel application on growth, stem anatomy, and ethylene production of *Acer platanoides* seedlings. *Scand. J. For. Res.* **1987**, *2*, 141–156.
149. Yamamoto, F.; Sakata, T.; Terazawa, K. Growth, morphology, stem anatomy and ethylene production in flooded *Alnus japonica* seedlings. *IAWA J.* **1995**, *16*, 47–59.
150. Yamamoto, F.; Sakata, T.; Terazawa, K. Physiological, anatomical and morphological responses of *Fraxinus mandshurica* seedlings to flooding. *Tree Physiol.* **1995**, *15*, 713–719.
151. Webb, T.; Armstrong, W. The effects of anoxia and carbohydrates on the growth and viability of rice, pea and pumpkin roots. *J. Exp. Bot.* **1983**, *34*, 579–603.
152. Pezeshki, S.R. Root responses of flood-tolerant and flood-sensitive tree species to soil redox conditions. *Trees* **1991**, *5*, 180–186.
153. Pezeshki, S.R.; DeLaune, R.D. Influence of sediment oxidation-reduction potential on root elongation in *Spartina patens*. *Acta Oecologia* **1990**, *11*, 377–383.
154. Bertani, A.; Brambilla, I. Effect of decreasing oxygen concentration on wheat roots: Growth and induction of anaerobic metabolism. *Z. Pflanzenphysiol.* **1982**, *108*, 283–288.
155. Lissner, J.; Mendelssohn, I.A.; Anastasiou, C.J. A method for cultivating plants under controlled redox intensities in hydroponics. *Aquat. Bot.* **2003**, *76*, 93–108.
156. Will, R.E.; Seiler, J.R.; Feret, P.P.; Aust, W.M. Effects of rhizosphere inundation on the growth and physiology of wet and dry -site *Acer rubrum* (red maple) populations. *Am. Midl. Nat.* **1995**, *134*, 127–139.
157. Pezeshki, S.R.; DeLaune, R.D.; Kludze, H.K.; Choi, H.S. A comparative study of gas exchange characteristics of cattail (*Typha domingensis*) and sawgrass (*Cladium jamaicense*) to soil redox conditions. *Aquat. Bot.* **1996**, *54*, 25–35.

158. Pezeshki, S.R.; DeLaune, R.D. Responses of seedlings of selected woody species to soil oxidation-reduction conditions. *Environ. Exp. Bot.* **1998**, *40*, 123–133.
159. Anderson, P.H.; Pezeshki, S.R. The effects of intermittent flooding on seedlings of three forest species. *Photosynthetica* **1999**, *37*, 543–552.
160. Elcan, J.M.; Pezeshki, S.R. Effects of flooding on susceptibility of *Taxodium distichum* seedlings to drought. *Photosynthetica* **2002**, *40*, 177–182.

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