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Total Nonstructural Carbohydrate Trends in Deeproot Sedge (*Cyperus entrerianus*)

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Native to temperate South America, deeproot sedge has naturalized throughout the southeastern United States. Often forming dense, homogenous stands, deeproot sedge has become widespread, invasive, and potentially harmful ecologically throughout the coastal prairie ecoregion of Texas. Possessing characteristics (rapid growth, generalized habitat requirements) of other weedy congeners (purple nutsedge and yellow nutsedge), its relatively recent expansion highlights the critical need to develop effective control techniques and strategies for this species throughout this endangered ecoregion. Research was performed to delineate total nonstructural carbohydrate (TNC) trends in deeproot sedge rhizomes for development of a phenologically based schedule for herbicide applications and mechanical treatments. Overall, TNC levels were greatest in May to August and lowest from October to January, regardless of study area. Apparently, deeproot sedge exerts little energy into seed production because TNC levels were continually replenished throughout the growing season. As such, foliar-herbicide application throughout the growing season should achieve total plant kill. Conversely, deeproot sedge rhizome TNC levels never fell below 30%, even during winter, which indicates that winter mechanical treatments or winter prescribed fires will not be effective because substantial rhizome reserves are present to support resprouting during the next growing season. Beyond a priori prevention, sequential herbicide applications combined with integrated, sequential, prescribed fire and herbicide treatments will be needed for long-term deeproot sedge control throughout its geographic range.

Nomenclature: Deeproot sedge, *Cyperus entrerianus* Boeck; purple nutsedge, *Cyperus rotundus* L.; yellow nutsedge, *Cyperus esculentus* L.

Key words: *Cyperus entrerianus*, deeproot sedge, herbicide timing, invasive, native, nonstructural carbohydrates, Texas Coastal Prairie, translocation.

Many "flat-sedges" (*Cyperus* spp.) are known as some of the world's most invasive, noxious weeds in both temperate and tropical, natural and crop-production areas (Bryson and Carter 2004; Chauhan and Johnson 2009; Stoller and Sweet 1987; Summerlin et al. 2000) because of their generalized soil requirements (Chauhan and Johnson 2009), occurrence in multiple ecotypes (Pena-Fronteras et al. 2009; Wilen et al. 1996), and their tremendous morphological, biological, and ecological plasticity (Bryson and Carter 2004; King 2011; Wilen et al. 1996). Deeproot sedge is a relatively recent addition to the worldwide list of invasive sedges (Carter 1990). Its success is also posited to be a result of its phytomorphological variability (King et al. 2012), generalized soil requirements, high survival rates (Carter 1990; Carter and Bryson 1996), and tremendous production (e.g., 1300 to 3200 kg ha^{-1}) of germinable seeds (King et al. 2012). Recent geographical distribution updates now report deeproot sedge occurring in bottomland hardwoods, coastal prairies, and mixed pine–hardwood forests, from Georgia and Florida, west to eastern Texas (Bryson and Carter 2004; Carter 1990; Carter and Bryson 1996; Rosen et al. 2006). In coastal regions, its expansion and naturalization is typically linked to rice (*Oryza sativa* L.) agriculture (Bryson and Carter 2004; Carter 1990; Carter and Bryson 1996), but regardless of region, it is typically found in areas frequently associated with other forms of anthropogenic disturbances (i.e., mowing, construction, vehicles, etc.) (Bryson and Carter 2004; Carter 1990; Carter and Bryson 1996; Rosen et al. 2006).

Much like its congener purple nutsedge, deeproot sedge may exist throughout its range in either several (not yet defined) ecotypes (Fuentes et al. 2010; Pena-Fronteras et al. 2009) or as an extremely morphologically and ecologically plastic species (Bryson and Carter 2003; Carter and Bryson

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1996; King et al. 2012). Regardless of its status, deeproot sedge naturalization success in a variety of soil types, hydrological conditions, and geographic locations amplifies the difficulty in developing universally applicable control and management strategies (Fuentes et al. 2010). However, developing such strategies is critical because its continued expansion and naturalization throughout the coastal prairie (King 2011; Rosen et al. 2006) threatens to further deteriorate this endangered ecoregion (Barrilleaux and Grace 2000; Grace et. al. 2000). To date, only King (2011) and Bryson and Carter (2003) have attempted to quantify deeproot sedge control success using a variety of techniques (e.g., herbicides, mowing, disking, etc.), but no work, to our knowledge, has attempted to unify control strategies with universally predictable physiological processes, such as rhizome total nonstructural carbohydrate (TNC) reserve trends.

Regardless of species, TNCs consist of starches (the primary storage carbohydrate), dextrin, fructosans, sucrose, and reducing sugars (Coyne and Cook 1970; Glerum 1980) that are mobilized and used when plants emerge from dormancy, when growth is most rapid, and when plants are producing reproductive organs, and they are replenished when these aforementioned processes slow or stop (Chapin et al. 1990; Conway et al. 1999; Robocker et al. 1972). TNC levels should vary predictably both seasonally and annually (Conway et al. 1999; Loescher et al. 1990), where development and production of reproductive organs and seeds, combined with demands of storage organs alter both TNC flow direction and intensity throughout the annual cycle (Wardlaw 1968). In perennial plants, translocation of TNCs to storage organs (i.e., roots and rhizomes) usually occurs after seed production and seed set, before dormancy, in preparation for next year's growth (Conway et al. 1999; Loescher et al. 1990; Pearcy et al. 1987; Smith et al. 1993; Sosebee 1984). Belowground TNC reserve levels are highly correlated with (1) resprouting and regrowth potential in rhizomatous species (Johnson et al. 2003), and (2) aboveground phenological development (Conway et al. 1999; Coyne and Cook 1970; Menke and Trlica 1981), the latter of which can be used to characterize plant health and guide plant control and management strategies (Conway et al. 1999; Johnson et al. 2003).

Regardless of species, delineating belowground TNC trends aids in predicting optimal herbicide application timing, although edaphic conditions as well as physiological, morphological, and phenological characteristics will all influence herbicide effectiveness (Muzik and Mauldin 1964; Sosebee 1984). For example, if herbicides are applied when TNCs are moving toward aboveground plant parts, herbicide movement will be limited, and only partial control will occur, minimizing the efficacy of such chemical control methods (Sosebee 1984). Conversely, by timing herbicide applications with downward TNC translocation, herbicides should be assimilated into the belowground zone and achieve total plant kill (Brady and Hall 1976; Sosebee 1984). Although TNC trends have historically been delineated for targeted herbicide application for focal plant species, recent research has focused on the interaction of herbicides and mowing, disking, and prescribed fire on achieving plant control (Adams and Galatowitsch 2006; Bradley and Hagood 2002; Lesica and Martin 2003; Mislevey et al. 1999, Renz and DiTomaso 2004; Smith et al. 1993; Summerlin et al. 2000). In contrast to herbicide applications, most mechanical control strategies (e.g., fire, mowing, disking, etc.) should focus on treatment implementation when rhizome TNC levels are most depleted, leaving few or no belowground reserves (Bradley and Hagood 2002; Lacey et al. 1994; Mislevey et al. 1999; Smith et al. 1993) to minimize resprouting and regrowth potential (Johnson et al. 2003).

Well-timed and coordinated delivery of both mechanical (i.e., when rhizome TNC levels are depleted) and chemical (i.e., when rhizome TNC levels are being replenished) treatments should reduce persistence and improve overall control of deeproot sedge. Using TNC trends to delineate potential windows of susceptibility to herbicide and mechanical control strategies for deeproot sedge is a novel approach, and no research, to our knowledge, has quantified this important ecophysiological characteristic for deeproot sedge. Therefore, the objective of this research was to quantify monthly TNC trends in deeproot sedge rhizome in Texas coastal prairie to delineate specific times for herbicide and other control treatment applications.

Materials and Methods

Study Area. The field portions of this research were conducted at The Nature Conservancy of Texas, Texas City Prairie Preserve (TCPP), Galveston County, Texas (29.44°N, 94.95°W), the U.S. Fish and Wildlife Service, Attwater Prairie Chicken National Wildlife Refuge (APCNWR), Colorado County, Texas (29.69°N, 96.30°W), and the Anahuac National Wildlife Refuge (ANWR)

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Chambers County, Texas (29.66°N, 94.44°W). All study areas occur within the coastal prairie ecoregion of Texas. Deeproot sedge coverage and extent, as well as phytomorphology and seed production, varied among study areas because of variation in soil types. Plants were typically larger and produced more seeds at TCPP than at either ANWR or APCNWR (King et al. 2012). Soils at study areas incorporated clays (ANWR, TCPP), silt loams (ANWR), silt clay loam (TCPP), fine sandy loam (APCNWR), and a complex (APCNWR) (Soil Survey 2011). All three sites consisted of similar vegetation.

Rhizome Collection. To capture seasonal and annual TNC trends, four rhizome samples were excavated and removed monthly from randomly selected deeproot sedge plants occurring in homogenous stands at each study area from August 2005 to July 2006. Total number and status (i.e., live or dead) of culms were counted on each clump before rhizome removal. As deeproot sedge phenology is variable, culm status was used as a surrogate for phenological stage (i.e., culm development, flowering, seed development, seed maturation, etc.). Once removed, rhizomes were put into labeled paper bags and placed on dry ice to prevent enzymatic degradation. Samples were then placed in a drying oven at 55 to 60 C until completely dried; after which, they were cleaned with brushes and sandpaper to prevent contamination during subsequent analyses by any foreign residue (Conway et al. 1999). A Wiley mill (Thomas Scientific, 1654 High Hill Rd, Swedesboro, NJ 08085), fitted with a 60-mesh screen, was used to grind the rhizomes into a powder, which was stored in an air-tight plastic container (Conway et al. 1999). Only clean, unblemished portions of the rhizomes were used for grinding to prevent contaminating samples with dirt or other foreign substances. All samples were kept in air-tight, plastic containers until used for TNC analysis.

Ground deeproot sedge rhizomes were subjected to the anthrone reagent procedure (Conway et al. 1999) to determine rhizome TNC concentration. Individual rhizome samples (four from each study area per month) were divided into two 0.5-g subsamples. Each subsample was digested in 60 ml of boiling 0.2N HCl in 300-ml flasks for 2 hr. After digestion, samples were cooled and filtered into 100-ml volumetric flasks using Whatman No. 2 filter paper (Whatman plc, Springfield Mill, James Whatman Way, Maidstone, Kent ME14 2LE, U.K.). Once filtered, each flask was brought to volume using distilled water. A 1-ml aliquot was then removed and placed into a 35-ml test tube containing 4-ml of distilled water. The test tube mixture was shaken using a Thermolyne vortex mixer (Thermo Scientific, 81 Wyman St., Waltham, MA 02451) until well mixed (30 s). A 1-ml aliquot was then removed from the original test tube and placed into another 35-ml test tube containing 10 ml of anthrone reagent. The new test tubes were shaken using the Thermolyne vortex mixer (30 s). The sample test tubes were then placed into a heater block for 17 min at 96 to 100 C; after which, they were removed and placed into a cold (22 C) water bath until they reached room temperature. Once at room temperature, samples were analyzed with a PerkinElmer (940 Winter St., Waltham, MA 02451) Lambda 3B ultraviolet/visible (UV/VIS) spectrophotometer set at 612 nm, using glucose as the standard.

Data Analysis. A two-way factorial analysis of covariance was used to examine differences in rhizome TNC levels among months (August 2005 through July 2006) and among study areas (i.e., TCPP, ANWR, and APCNWR). The proportion of alive deeproot sedge culms was used as a covariate. If interactions ($P < 0.05$) occurred among study areas and months, subsequent analyses were performed within each study area individually. In all analyses, if differences ($P < 0.05$) occurred, least-squares mean separation was used to more-closely examine those differences (SAS Institute 2003; Zar 1999).

Results and Discussion

Overall, TNC concentrations of deeproot sedge varied among months ($F = 12.28$, df = 11–100; $P < 0.001$), was similar among study areas ($F = 1.33$, df = 2–100; $P = 0.268$), but a study area by month interaction ($F = 3.86$, df = 22–100; $P < 0.001$) occurred (Figure 1). The proportion of alive deeproot sedge culms was never an important covariate ($F = 0.14$, df = 1–100; $P = 0.714$). For all study sites combined, rhizome TNC concentrations were greatest from May through August and was least from October through January (Figure 1), corresponding to periods in which most culms were alive or dead, respectively (Figure 1). Because of the aforementioned interaction, all subsequent analyses examined TNC concentration among months, within each study area. At ANWR, TNC concentration of deeproot sedge rhizome varied among months ($F = 7.37$, df = 11–33;

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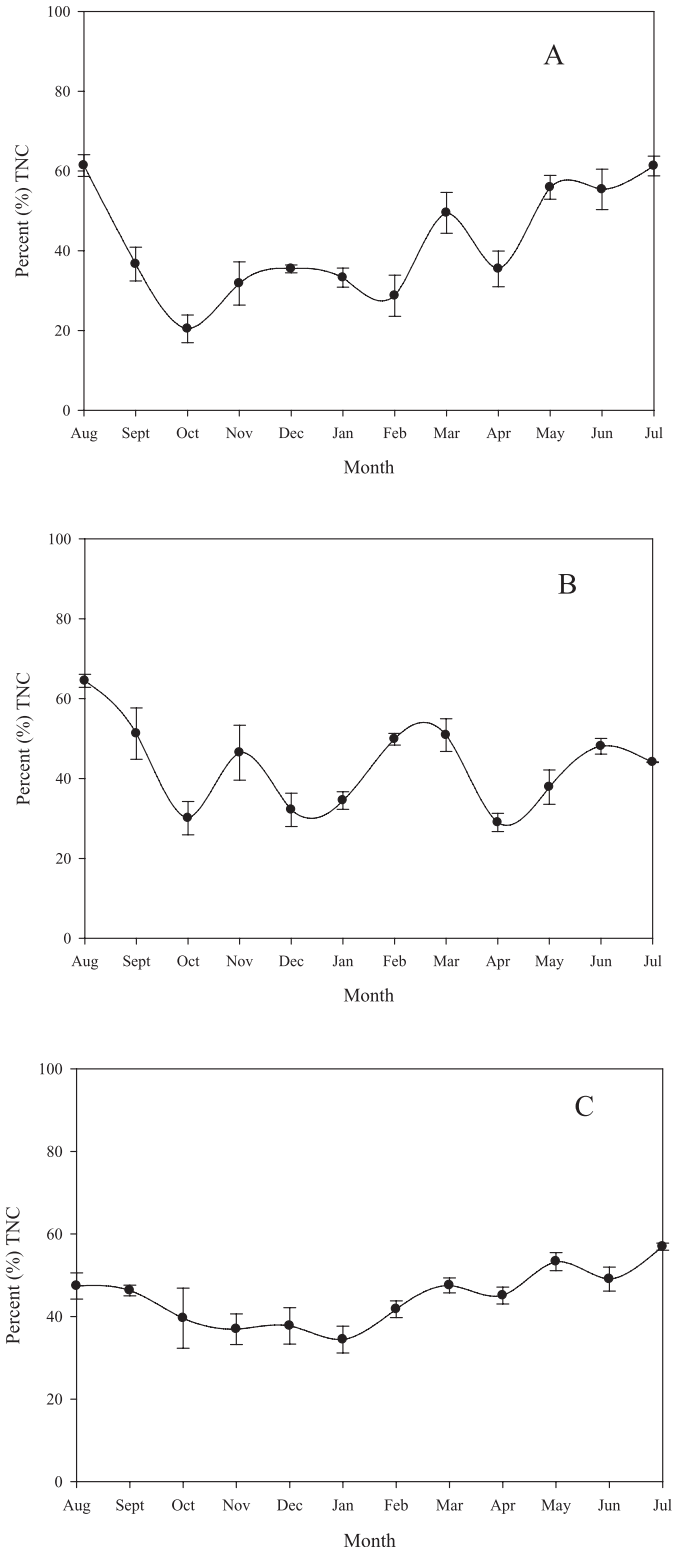


Figure 1. Total nonstructural carbohydrate (TNC) concentrations (%) (with SE) of deeproot sedge rhizomes collected monthly at (A) the Anahuac National Wildlife Refuge (Chambers County), (B) Attwater Prairie Chicken National Wildlife Refuge (Colorado County), and (C) Texas City Prairie Preserve (Galveston County), Texas, August 2005 to July 2006.

$P < 0.001$), and the proportion of deeproot sedge culms alive was not an important covariate ($F = 0.06$, df = 1–33; $P = 0.810$) (Figure 2). Again, rhizome TNC concentrations were greatest from May through August, and were lowest from October through February (Figure 2). At APCNWR, TNC concentration of deeproot sedge rhizome varied among months ($F = 8.30$, df = 11–32; $P < 0.001$), and the proportion of deeproot sedge culms alive was not an important covariate ($F = 0.15$, df = 1–325; $P = 0.699$) (Figure 2). Peak rhizome TNC concentrations were slightly inconsistent with other study areas (Figure 2), where concentrations were greatest during August and September and during March and April. At TCPP, TNC concentration of deeproot sedge rhizome varied among months ($F = 3.51$, df = 11–33; $P = 0.003$), and the proportion of deeproot sedge culms alive was not an important covariate ($F = 0.53$, df = 1–33; $P = 0.474$) (Figure 2). Rhizome TNC concentrations were greatest from May through August, and the concentrations reached their lowest values during October through January (Figure 2).

TNC concentrations of deeproot sedge rhizome generally declined during autumn and then stabilized during winter, increased in early spring, declined for a short period during the early growing season, and then increased and stabilized for the remainder of the growing season, until declines were observed during the late growing season and autumn. Although other elements of deeproot sedge biology appeared to be sensitive to edaphic and local site conditions (i.e., seed yield and production models, seed germination, total plant height, phytomorphology, etc.) (King et al. 2012), and TNC patterns (not estimated concentrations) tended to consistently increase during July to August. Site variability (i.e., soil moisture conditions) is known to influence *Cyperus* germination (Chauhan and Johnson 2009), biomass of rhizomes and TNCs (Pena-Fronteras et al. 2009), and seed production and phytomorphology (King et al. 2012). As such, estimated TNC concentrations (not patterns or trends) did vary among sites in this study, where rhizome TNC concentrations were lowest at TCPP, which tended to be a wetter study area, and had the tallest plants, greatest seed biomass production, and greatest germination rates (King et al. 2012). Apparently, deeproot sedge does differentially allocate TNC reserves, (potentially based on soil moisture); however, such variation may be driven by site-specific features not fully characterized in this study (Chauhan and Johnson 2009; Fuentes et al. 2010; Pena-Fronteras et al. 2009). Regardless of

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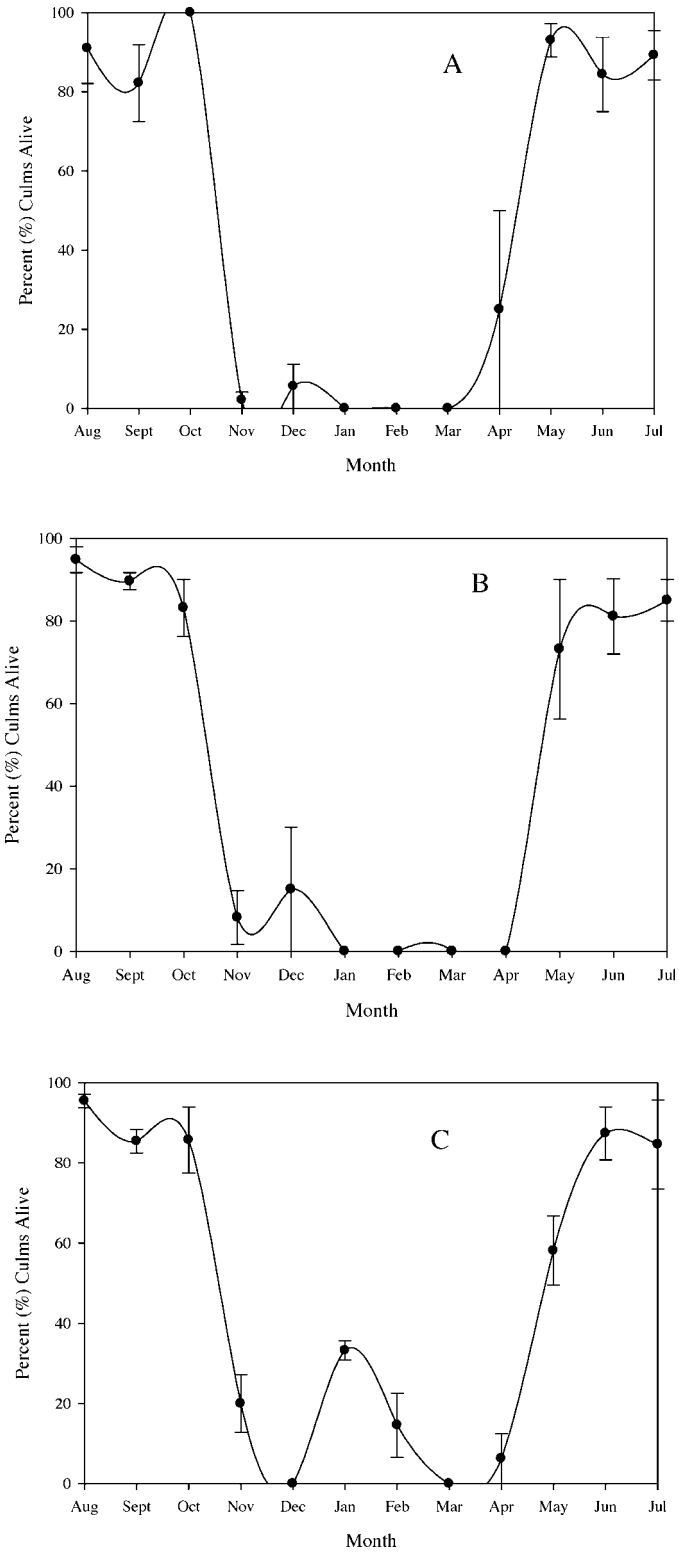


Figure 2. Proportion (%) of deeproot sedge culms alive collected monthly at (A) the Anahuac National Wildlife Refuge (Chambers County), (B) Attwater Prairie Chicken National Wildlife Refuge (Colorado County), and (C) Texas City Prairie Preserve (Galveston County), Texas, August 2005 to July 2006.

site-specific variability, TNC trends in this study, which identified temporal windows in which deeproot sedge may be susceptible to herbicide and physical control and management, will be useful for developing control prescriptions for deeproot sedge throughout its geographic range.

If herbicide applications are timed to coincide with periods of downward translocation of TNCs (i.e., from aboveground biomass to belowground rhizomes), herbicides will be assimilated throughout the entire plant, translocated to the rhizomes, and should exert the desired phytotoxic effect. Increases in rhizome TNCs during much of the growing season confirm the relative success in controlling deeproot sedge with herbicide treatments applied during both the early and late growing season, effectively reducing both deeproot sedge frequency and cover (King 2011). Similarly, late growing-season herbicide applications have been effective in controlling other exotic invasive nonwoody species, such as purple nutsedge (Reddy and Bryson 2009), torpedograss (*Panicum repens* L.) (Smith et al. 1993), medusahead [*Taeniatherum caput-medusae* (L.) Nevski] (Sheley et al. 2007), and leafy spurge (*Euphorbia esula* L.) (Mitchell et al. 2007). Conversely, if herbicides are applied during times in which deeproot sedge rhizome TNCs are stable or are being transported to aboveground biomass (during October to February), herbicides will not be assimilated throughout the plant. Such treatments would achieve only a burning or "topkill." For example, Troxler et al. (2003) demonstrated that foliar-applied herbicides were not delivered to rhizomes when purple and yellow nutsedges were in the six-leaf stage, analogous to the very early growing season for deeproot sedge. During late winter and early growing season, deeproot sedge is delivering rhizome TNCs aboveground to support its increasing leaf area. In sum, TNC levels were lowest during this temporal window, and herbicides delivered during this period would not achieve the desired plant kill, although this needs to be confirmed through testing.

Disconcerting from a management perspective, however, actual concentrations of deeproot sedge rhizome TNC levels are (1) comparatively greater throughout the annual cycle than they are in purple nutsedge (Fuentes et al. 2010; Pena-Fronteras et al. 2009), and (2) relatively high during winter. Although estimated concentrations were lowest during winter (as compared with the rest of the annual cycle), rhizome TNC concentrations never fell below 30%, clearly indicating that deeproot

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sedge has sufficient belowground reserves to initiate regrowth (1) in spring, or (2) any time during the growing season if aboveground biomass is removed. For example, deeproot sedge exposed to prescribed fire during the dormant season did not have long-term reductions in cover or frequency (King 2011) because only aboveground biomass was removed and the plants have plenty of stored reserves for regrowth, and increases in both frequency and cover were observed (King 2011). From a management perspective, these carbohydrate trends corroborate the general failure of February prescribed burns to reduce deeproot sedge cover (King 2011).

Interestingly, the proportion of live culms was never an important covariate in this study. The notion that production of living, aboveground, reproductive portions of deeproot sedge would have a negative influence on the assimilation or accumulation of rhizome TNCs was not supported. For example, Conway et al. (1999) found that TNCs in Chinese tallowtree [*Triadica sebifera* (L.) Small] are typically moving outward from the roots during most of the growing season until late summer to autumn. Only after Chinese tallowtree has developed seeds and the seeds are beginning to "ripen," do TNCs begin to be assimilated into the roots again (before leaf senescence), which only gives a relatively short period for effective foliar herbicide applications. Conversely, deeproot sedge apparently does not invest much stored TNCs from the rhizomes into culm or seed production and is evidently able to support most aboveground growth by current photosynthate. Despite tremendous seed production on an area basis, individual plants only produce up to 2 g of seed culm^{-1} (King et al. 2012). In contrast to other perennial plants, deeproot sedge achieves positive rhizome reserve accumulation throughout the growing season, which extends and elongates the temporal window of susceptibility to singular or sequential foliar herbicide efforts.

Regardless of herbicide used in attempts to control deeproot sedge, based on other studies, herbicide applications should be timed following TNC allocation patterns described here. Because deeproot sedge is steadily translocating TNCs toward rhizomes during the growing season, an extended temporal window exists to optimize total plant kill. Although singular herbicide treatments initially reduce deeproot sedge coverage at any given site, such single treatment will not succeed (see King 2011). Either sequential herbicide applications or integrated, sequential prescribed fire and herbicide treatments will be needed for long-term control throughout the geographic range of this species. In any comprehensive management strategy, land managers must recognize that deeproot sedge (1) seed production is tremendous, (2) germination rates are high (King et al. 2012), and (3) rhizome TNC concentrations are substantial (> 30%), whereby sequential, repeated, and targeted herbicide, mowing, or prescribed fire treatments or combinations of these treatments will be necessary for long-term seed bank depletion to prevent regrowth and resprouting (King 2011).

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