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Photosynthetic assimilation and carbohydrate allocation of *Quercus rubra* seedlings in response to simulated herbivory

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Abstract

• **Introduction** The artificial regeneration of oaks (*Quercus* spp.) can supplement deficient natural regeneration, yet growth and physiology of newly planted seedlings are often negatively affected by animal herbivory. Alternative nursery stock types with improved stress resistance may help improve regeneration success.

• **Materials and method** 1-year-old bare-root (1+0) and container (164 mL) northern red oak (*Quercus rubra* L.) seedlings were transplanted into pots, subjected to two simulated browsing treatments (dormant or summer) or a non-browsed control, and grown for 18 weeks in a greenhouse.

• **Results** Although the container seedlings had 25% higher photosynthetic rates compared to bare-root seedlings and greater proportional increases in biomass and total non-structural carbohydrates (TNC), stock type differences to herbivory stress were deemed negligible based upon the absence of treatment interactions for any parameter. Summer browsing increased the rates of photosynthesis by 22%, but whole-tree photosynthetic rates did not differ across browse treatments. Summer-browsed seedlings had lower lateral root biomass and severely depleted root TNC stores, resulting in a reduced whole-tree TNC content at final harvest; dormant-browsed seedlings did not differ from control seedlings in photosynthetic rates, biomass, or TNC content.

• **Conclusion** Results suggest that, irrespective of stock type, dormant browsing has little impact on the morpho-

logical and physiological development of northern red oak seedlings, while summer browsing is highly detrimental.

Keywords Animal browse · Northern red oak · Non-structural carbohydrates · Planting stock types · Reforestation

1 Introduction

Landscape changes and elimination of predators have led to high populations of white-tailed deer (*Odocoileus virginianus* Zimmerman) in the Central Hardwoods Forest Region of the U.S., which have had severe negative impacts on the natural forest regeneration of some species, such as oaks (*Quercus* spp.) (Johnson et al. 2002). The impacts of herbivory on regeneration can be detrimental to resulting ecosystem composition and structure (Casabon and Pothier 2007; Horsley et al. 2003). The declining oak populations in this region associated with herbivory and land use changes have prompted an increased interest in the planting of these species, yet field establishment success is often limited (Dey et al. 2008; Jacobs et al. 2004).

Deer herbivory may alter seedling physiological status and growth responses variably depending upon the timing and severity of browse. Browse during dormancy removes the terminal bud, which releases apical dominance and stimulates lateral bud flushing (Cline 1997), often resulting in an increased leaf area. Oaks expend most of their stored non-structural carbohydrates (TNC) in the first flush (Kruger and Reich 1993), so regrowth of the leaf area after browsing of newly expanded leaves depends upon lower energy reserves (Carpenter et al. 2008). Following browsing, photosynthetic rates of both residual and new foliage

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are often higher (Kruger and Reich 1993; Tschaplinski and Blake 1989a). Altered photosynthetic rates may be a result of increased root to shoot ratios (Kruger and Reich 1993) or greater sink demand in storage tissues (Tschaplinski and Blake 1989b). Increased photosynthetic rates following browse may compensate for the loss of TNC during regrowth of the leaf area. For example, defoliation of poplars (*Populus* spp.) reduced TNC concentrations in roots but the trees recovered by the end of the growing season (Kosola et al. 2001). However, Kays and Canham (1991) found that TNC declined in saplings of various hardwood species that had shoots removed during the growing season.

In addition to the physiological changes, herbivory can affect seedling morphological development. Simulated browsing on silver birch (*Betula pendula* Roth) reduced leaf mass and overall growth (Berström and Danell 1995). The loss of leaf area can also lead to reductions in root growth through less fine root production and/or increased root mortality (Eissenstat and Duncan 1992; Ruess et al. 1998). Repeated browsing may result in prolonged stunted growth and/or mortality.

Seedling morphological and physiological quality, which is largely determined by nursery production practices, determines resistance to stresses such as herbivory (Burdett 1990). Bare-root nurseries efficiently produce large seedlings of northern red oak (*Quercus rubra* L.) and other hardwoods; however, the loss of fine roots and disruption of root–soil contact during lifting can adversely affect the physiological status after planting associated with reduced water potential, photosynthetic rates, and non-structural carbohydrates (Guehl et al. 1989, 1993; Jacobs et al. 2009). Additionally, oak seedlings exhibit rhythmic root and shoot growth, where root growth declines as shoot growth is maximized, and root growth is highest when shoot growth ceases (Reich et al. 1980; Willaume and Pages 2006). This pattern is a product of the balance of roots and shoots (Borchert 1975; Reich et al. 1980), which may be substantially altered by lifting of the bare-root seedlings. The reduced root size relative to the shoots of bare-root seedlings provides a plausible explanation for the minimal height growth (Andersen et al. 2000; Struve and Joly 1992) and die back (Johnson et al. 1984; Wilson et al. 2007) of bare-root seedlings that is often noted during the first season after planting, which persists until the balance is restored.

Container seedlings offer an alternative to bare-root stock types that may improve the resistance of northern red oak seedlings to herbivory and other stresses (Wilson et al. 2007). Because roots of container seedlings are protected by growing media, root loss is minimized during production and lifting (McKay 1996), which helps maintain root–soil contact and promotes fibrous root systems. The increased water and nutrient uptake associated with fibrous root systems (Blake and Sutton 1987; Irdis et al. 2004) explains

improved water relations, higher photosynthetic rates, and accelerated growth rates frequently observed in container seedlings (Wilson et al. 2007; Zaczek et al. 1996). Both stored carbohydrates and current photosynthate contribute to new root proliferation in transplanted northern red oak seedlings (Sloan and Jacobs 2008). Because browsing inhibits new root growth (Eissenstat and Duncan 1992; Ruess et al. 1998), which limits photosynthesis and vice versa (Burdett 1990), the improved physiological status and greater root absorptive capacity of container seedlings following transplant may minimize the effects of herbivory stress on seedling development.

Despite the impact of herbivory on oak regeneration, relatively little research has examined interactions between timing of browse and seedling development during the critical field establishment phase. Furthermore, although container seedlings have shown potential to alleviate transplant stress and improve early field growth of northern red oak seedlings (Wilson et al. 2007), their capacity to specifically help reduce impacts of browsing stress has not been investigated. Thus, this study examined the effects of simulated browsing at varying seasonal periods (i.e., dormant vs. summer) for two common nursery stock types used in this region (i.e., 1+0 bare-root or 164-ml container seedlings) on seedling growth and biomass allocation, TNC status, and photosynthetic assimilation. This knowledge is needed to improve understanding of the physiological impacts of herbivory on northern red oak seedlings, mechanisms that seedlings have evolved to resist browsing stress, and potential for alternative stock types to help alleviate impacts of herbivory. We hypothesized that (1) larger initial root to shoot, coupled with reduced transplant stress, of container seedlings (vs. bare-root stock) would lead to less expression of injury from herbivory associated with a more rapid ability to recover from incurred stresses, and (2) season of herbivory would create variable effects on seedling response to browse (based on timing of translocation of carbohydrate reserves), which would be most detrimental for summer-browsed bare-root stock due to the reliance of these seedlings mainly on stored reserves.

2 Material and methods

2.1 Plant material

The two experimental stock types were each grown from acorns collected from a stand of open pollinated trees located at the Indiana Department of Natural Resources State Tree Nursery near Vallonia, IN, USA (38°48' N, 86° 06' W). Container seedlings were sown in May 2008 into Styroblock™ containers (Superblock 10, Beaver Plastics, Edmonton, AB, Canada) with a cavity volume of 164 ml,

depth of 15.2 cm, and a top diameter of 4.2 cm, and operationally grown for 6 months at the University of Idaho Center for Forest Nursery and Seedling Research in Moscow, ID, USA (41°43' N, 117°00' W) following methods similar to Wenny and Dumroese (1994). In November 2008, the seedlings were placed in storage at a temperature of approximately 1°C. In early March 2009, they were shipped to Purdue University in West Lafayette, IN, USA (40°25' N, 86°55' W) and stored at 3°C until transplanting. Bare-root seedlings were operationally grown (Jacobs 2003) for 1 year at a density of 48 seedlings per square meter at the Indiana Department of Natural Resources State Tree Nursery. They were lifted in December 2008 and stored in moist wood shavings at a temperature of 3.3°C until transplanting.

2.2 Statistical design, treatments, and data analysis

This study was a completely randomized design using a factorial treatment structure of two stock types and three levels of simulated browse. There were five seedlings per treatment combination for a total of 30 seedlings; the sampling unit was an individual seedling and the experimental unit was defined as the mean response of each treatment replicate. The seedlings were transplanted in early May 2009 into 12-L containers with a rooting medium consisting of peat, perlite, and sand in equal portions. Additionally, 45 g of controlled-release fertilizer (Osmocote® Plus, NPK 15-9-12, with trace elements, The Scotts Company, Marysville, OH, USA) was uniformly incorporated into the medium. The potted seedlings were then randomly placed on a single greenhouse bench in the Horticulture and Landscape Architecture Plant Growth Facility at Purdue University and watered to saturation every 3–5 days during the course of the study.

The treatment levels for the simulated browse were based upon findings of Healy (1971) and Crawford (1982), who observed that the primary deer browsing periods on woody plants are during winter and late spring. Thus, the three simulated browse treatment levels were control (no browse), dormant browse, and summer browse. In the dormant browsing treatment, the terminal bud cluster of every main and lateral stem was removed (by clipping) during dormancy using hand clippers. To standardize the summer browsing treatment with seedling physiological status, the *Quercus* Morphological Index (QMI) was used. The QMI was developed by Hanson et al. (1986) to characterize specific stages of seedling growth. According to the QMI the 1-lag stage is longer than other stages in the first flush, so there is a higher likelihood that all of the stock types will simultaneously be in the 1-lag stage. The summer browsing treatment removed (clipped) 100% of the current year's growth at the 1-lag stage.

Data analyses were performed using analysis of variance (ANOVA) in SAS (version 9.1, SAS Institute Inc., Cary, NC, USA). Repeated measures ANOVA was used to analyze gas exchange data only. All models were tested for assumptions concerning normality, constant variance and linearity, with transformations applied as needed. Tests comparing treatment means were performed at $\alpha=0.05$ using Tukey's HSD conservative test.

2.3 Measurements

Prior to transplanting, a sample of 15 seedlings from each stock type was randomly selected to determine the initial seedling morphological and physiological conditions. Measurements of height, root collar diameter (RCD), root volume, first-order lateral roots (FOLR), and root to shoot ratio were performed. Additionally, the TNC were measured based on methods described by Chow and Landhauser (2004). Briefly, sugar was extracted from samples using hot ethanol, and starch was digested to glucose hydrolysate with α -amylase/amyloglucosidase enzyme solution. Concentrations of sugar and glucose hydrolysate were then determined with a spectrophotometer.

After transplanting, the seedling growth stages were monitored by measuring the shoot elongation and leaf expansion of the second to the last leaf from the top of the flush (Hanson et al. 1986). When the seedlings reached the 1-lag stage, gas exchange (i.e., photosynthesis and transpiration) was measured at midday (1100–1400 hours) at near weekly intervals using a portable gas exchange analyzer (LI-6400, LI-COR Biosciences, Lincoln, NE, USA). Chamber conditions were set to near ambient greenhouse conditions (block temperature=25°C, CO₂ concentration=375 $\mu\text{mol mol}^{-1}$, light=400 $\mu\text{mol m}^{-2} \text{s}^{-1}$, relative humidity=70%). Whole-tree photosynthetic rates were calculated by expanding the last photosynthesis measurement to the destructively sampled seedling leaf area. Water use efficiency (WUE) was calculated as the ratio of assimilation to transpiration.

At the conclusion of the study in September 2009, all the seedlings were harvested and measured for height, RCD, root volume, FOLR, leaf area, and root to shoot ratio. The total non-structural carbohydrates were also analyzed using the same methods as described in the analysis for the initial samples.

3 Results

3.1 Initial seedling characterization

At the time of transplant, bare-root seedlings were significantly larger than container seedlings ($P<0.0001$) in height (77%), RCD (42%), root volume (76%), FOLR (59%), shoot dry weight (91%), taproot dry weight (82%),

and lateral root dry weight (60%) (Table 1). Container seedlings, however, had significantly ($P<0.0001$) larger root to shoot ratios (50%). Analysis of the TNC concentration (mg/g dry weight) showed no significant differences between the container and bare-root seedlings. Due to their greater biomass, bare-root seedlings had significantly ($P<0.0001$) higher TNC content (Table 1).

3.2 Gas exchange

Photosynthetic rates through the growing season were significantly affected by stock type ($P=0.0009$) and browse ($P=0.0150$), though not by sampling time or any interaction between treatments. Container seedlings had photosynthetic rates that were 25% greater than bare-root seedlings (Fig. 1). Summer-browsed seedlings had the highest photosynthetic rates with a 17% and 24% increase over control and dormant-browsed seedlings, respectively (Fig. 1). Treatments did not differ significantly for WUE. Whole-tree photosynthetic rates at the end of the growing season were significantly affected by stock type ($P=0.0086$) only. Whole-tree photosynthetic rates for bare-root seedlings were 48% greater than for container seedlings (Fig. 2).

3.3 Final seedling characterization

No seedling response variables at final harvest were significantly affected by treatment interactions. However, bare-root seedlings were significantly ($P<0.0001$) larger

than container seedlings in height (72%), RCD (27%), root volume (68%), FOLR (60%), leaf area (47%), shoot dry weight (62%), taproot dry weight (73%), and lateral root dry weight (61%) (Table 1). Consistent with initial characteristics, root to shoot ratios were higher in container seedlings (44%). In regard to browsing treatments, control seedlings had significantly ($P<0.0001$) greater lateral root dry weight (33%) and root to shoot ratio (77%) compared to summer-browsed seedlings (Table 2).

At final harvest, there were no significant differences in TNC concentration between stock types (Table 1) or among browse treatments (Table 2). TNC content, however, was significantly ($P<0.0001$) influenced by stock type, with bare-root seedlings having 367% higher TNC content than container seedlings (Table 1). TNC content was also significantly ($P=0.0114$) influenced by browse treatment; unclipped control seedlings had 90% greater TNC content than summer-browsed seedlings (Table 2).

Container seedlings had the largest mean percent increases in height, RCD, root volume, FOLR, shoot dry weight, taproot dry weight, and TNC of all components (shoot, taproot, lateral root, and whole tree) compared to the initial sample (Table 3). Summer-browsed seedlings had the lowest mean percent increases in all morphological characteristics and TNC of all the components compared to the initial sample (Table 4). Notably, the percentage increases of TNC in tap and lateral roots were negative for summer-browsed seedlings (Table 4).

Table 1 Mean ($\pm 95\%$ CL) HT, RCD, RV, number of FOLR, LA, SDW, TRDW, LRDW, R:SDW, and whole-tree concentration and content of TNC at time of planting (initial measurements) and at harvest (final measurements) for stock type treatments (container and bare-root seedlings)

	Initial measurements		Final measurements	
	Container	Bare-root	Container	Bare-root
HT (cm)	16 \pm 11 b	66 \pm 11 a	23 \pm 13 b	81 \pm 13 a
RCD (mm)	4.0 \pm 1.1 b	7.0 \pm 1.1 a	6.8 \pm 1.5 b	9.4 \pm 1.5 a
RV (cm ³)	5.5 \pm 3.3 b ^a	22.9 \pm 6.6 a ^a	18 \pm 19 b	56 \pm 19 a
FOLR	1.7 \pm 2.1 b	4.1 \pm 2.1 a	3.6 \pm 5.1 b	9.0 \pm 5.1 a
LA (cm ²)	– ^b	– ^b	334 \pm 246 b	633 \pm 246 a
SDW (g)	0.6 \pm 0.6 b ^a	6.6 \pm 0.9 a ^a	2.0 \pm 1.5 b ^a	12.9 \pm 4.0 a ^a
TRDW (g)	2.2 \pm 2.5 b	12.1 \pm 2.6 a	4.9 \pm 5.6 b	17.9 \pm 5.6 a
LRDW (g)	0.3 \pm 0.3 b	0.8 \pm 0.3 a	1.0 \pm 1.3 b ^a	2.7 \pm 2.1 a ^a
R:SDW	4.0 \pm 0.9 a	2.0 \pm 0.8 b	2.9 \pm 0.7 a	1.6 \pm 0.7 b
TNC (mg g ⁻¹)	158 \pm 31 a	145 \pm 31 a	105 \pm 24 a	100 \pm 24 a
TNC (mg)	540 \pm 696 b	2,850 \pm 696 a	1,105 \pm 1,165 b	4,057 \pm 1,209 a

Different letters indicate significant treatment differences at $\alpha=0.05$ across stock type treatments within a sampling period

CL confidence level, HT height, RV root volume, LA leave area, SDW shoot dry weight, TRDW taproot dry weight, LRDW lateral root dry weight, R:SDW root to shoot dry weight ratio

^a Values were back transformed

^b Values were not determined

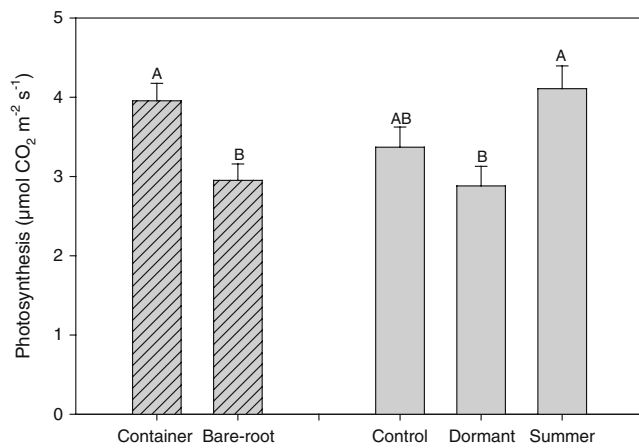


Fig. 1 Photosynthetic rates of seedlings 1, 2, 5, and 6 weeks after reaching lag-1 stage for stock type (lined bars) and browse (solid bars) treatments. Bars represent treatment means pooled from the four measurement points and error bars represent standard errors. For either stock type or browse, different letters indicate significant differences at $\alpha=0.05$

4 Discussion

4.1 Nursery stock type responses

Bare-root seedlings had greater biomass and TNC content than container seedlings at the initiation and end of the study (Table 1), although container seedlings had higher mean percent increases for these parameters (Table 3). We also observed higher gas exchange rates of container vs. bare-root seedlings (Fig. 1). With greater proportions of fine and lateral roots, container seedlings had increased water absorption capacity, which improved CO₂ assimilation rates (Kruger and Reich 1993).

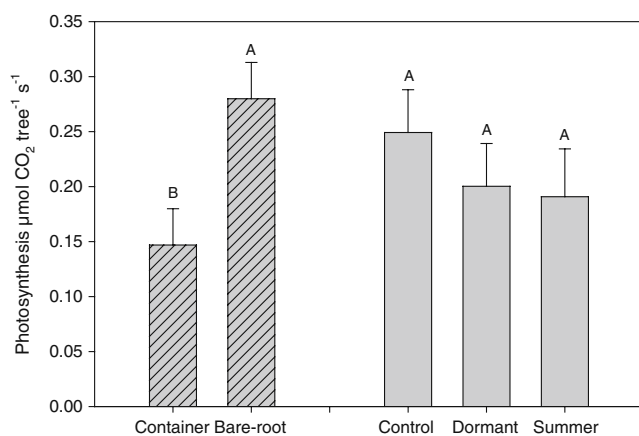


Fig. 2 Whole-tree photosynthetic rates determined from photosynthesis measurements taken 6 weeks after reaching lag-1 stage for stock type (lined bars) and browse (solid bars) treatments. Bars represent standard errors. For either stock type or browse, different letters indicate significant differences at $\alpha=0.05$

Table 2 Mean ($\pm 95\%$ CL) HT, RCD, RV, number of FOLR, SDW, TRDW, LRDW, R:SDW, and whole-tree concentration and content of TNC at harvest (final measurements) for seedlings subjected to three simulated browse treatments (control, dormant, and summer)

	Browsing treatment		
	Control	Dormant	Summer
HT (cm)	55 \pm 16 a	55 \pm 15 a	46 \pm 16 a
RCD (mm)	8.5 \pm 1.8 a	8.5 \pm 1.8 a	7.4 \pm 1.8 a
RV (cm ³) ^a	44 \pm 24 a	42 \pm 24 a	26 \pm 24 a
FOLR	7.7 \pm 6.3 a	7.0 \pm 6.0 a	4.0 \pm 6.4 a
LA (cm ²)	524 \pm 307 a	577 \pm 290 a	349 \pm 307 a
SDW (g) ^a	6.9 \pm 3.5 a	7.0 \pm 3.5 a	4.9 \pm 3.0 a
TRDW (g)	13.1 \pm 7.1 a	12.5 \pm 6.7 a	8.6 \pm 7.1 a
LRDW (g) ^a	3.0 \pm 2.8 a	1.7 \pm 2.0 ab	1.0 \pm 2.0 b
R:SDW	2.6 \pm 0.9 a	2.1 \pm 0.9 ab	2.0 \pm 0.9 b
TNC (mg g ⁻¹)	107 \pm 30 a	100 \pm 30 a	100 \pm 30 a
TNC (mg)	3,136 \pm 1,452 a	2,877 \pm 1,452 a	1,730 \pm 1,452 b

Different letters indicate significant differences across browsing treatments at $\alpha=0.05$

CL confidence level, HT height, RV root volume, SDW shoot dry weight, TRDW taproot dry weight, LRDW lateral root dry weight, R:SDW root to shoot dry weight ratio

^a Values were back transformed

More rapid early growth rates of container compared to bare-root seedlings have been observed previously for northern red oak (Johnson et al. 1984; Wilson et al. 2007). In our case, however, although container stock grew more relative to original size, as is typical with seedlings of variable initial size (see van den Driessche 1992 and references therein), absolute growth was greater for bare-root seedlings (e.g., 6.3 vs. 1.4 g in shoot dry weight, Table 1). Additionally, bare-root seedlings had higher whole-tree photosynthetic rates associated with increased leaf area (Fig. 2) and no differences were detected in WUE. Thus, our data does not support evidence for reduced transplant stress of container seedlings under the present study conditions (i.e., well watered and subjected to variable browsing treatments). Furthermore, the lack of treatment interactions for any of the tested parameters suggests stock type responses to browsing are similar. Responses may vary, however, when seedlings are exposed to moderate or severe drought under field conditions.

4.2 Influences of simulated herbivory

Summer-browsed seedlings were generally smaller than control and dormant-browsed seedlings at the final harvest; they had significantly lower lateral root dry weight (67%) and root to shoot ratios (23%) than control seedlings (Table 2). Similarly, other studies have noted that the

Table 3 Mean percent increases (based upon initial sample) for HT, RCD, RV, number of FOLR, SDW, TRDW, LRDW, R:SDW and STNC, TRTNC, LRTNC, and WTTNC for stock type treatments (container and bare-root seedlings)

	Stock type treatment	
	Container	Bare-root
HT (cm)	44%	23%
RCD (mm)	72%	34%
RV (cm ³)	226%	145%
FOLR	113%	120%
SDW (g)	238%	96%
TRDW (g)	125%	48%
LRDW (g)	226%	239%
R:SDW	-29%	-21%
STNC (mg)	391%	141%
TRTNC (mg)	138%	102%
LRTNC (mg)	533%	197%
WTTNC (mg)	105%	42%

HT height, RV root volume, SDW shoot dry weight, TRDW taproot dry weight, LRDW lateral root dry weight, R:SDW root to shoot dry weight ratio, STNC total non-structural carbohydrates of shoot, TRTNC total non-structural carbohydrates of taproot, LRTNC total non-structural carbohydrates of lateral root, WTTNC total non-structural carbohydrates of whole tree

removal of leaf area decreased fine root production (Ruess et al. 1998) or increased root mortality (Eissenstat and Duncan 1992). Reduction in root growth of newly planted seedlings may contribute to transplant stress and potentially result in mortality (Grossnickle 2005). Less leaf area associated with summer browsing may be caused by a lack of energy for leaf expansion; northern red oak seedlings have been observed to expend most of their stored TNC during the first flush (Kruger and Reich 1993). Removal of this new growth by browse or other mechanical injury forces seedlings to further deplete stored carbohydrates, principally from root systems in northern red oak (Sloan and Jacobs 2008). Correspondingly, summer-browsed seedlings showed negative percent increases for TNC in tap and lateral roots (Table 4), leading to significantly lower whole-tree TNC than summer-browsed or control seedlings (Table 2).

Though summer-browsed seedlings were smaller than control and dormant-browsed seedlings, they had significantly higher gas exchange rates (Fig. 1). A reduction in leaf area for summer-browsed seedlings suggests an increased ratio of root absorption to leaf area, but the significantly smaller root to shoot ratios and lower lateral root dry weights (Table 2) of summer-browsed seedlings do not support the inference of Kruger and Reich (1993) that higher root to shoot ratios account for increased photosynthetic rates. Tschaplinski and Blake (1989b) found that

increased sink demand may also play a role in higher photosynthetic rates of summer-browsed seedlings. When photosynthetic rates were expanded to a whole-tree basis, summer-browsed seedlings did not significantly differ from the other browse treatments due to a reduced leaf area (Table 2). A decreased leaf area and less time with mature leaves are likely causes of reduced growth and TNC content of summer-browsed seedlings.

In contrast to results observed for summer browsing, dormant browsing did not influence seedling morphology and physiology (Table 2; Figs. 1 and 2). Removal of the terminal bud cluster resulted in the loss of only nominal amounts of TNC content; lateral buds flushed to replace leaves that would have emerged from the terminal bud cluster. However, removing the terminal bud cluster did not produce significantly greater leaf area associated with release from apical dominance (Table 2), indicating little change from control seedlings in root to shoot ratios and/or sink demand.

5 Conclusions

This study demonstrated the effects of varying stock types and simulated browsing on northern red oak seedling physiological development and growth allocation. Contrary to our original hypothesis, we detected little evidence of increased resistance to herbivory stress in container stock.

Table 4 Mean percent increases (based upon initial sample) for HT, RCD, RV, number of FOLR, SDW, TRDW, LRDW, R:SDW and STNC, TRTNC, LRTNC, and WTTNC for seedlings subjected to three simulated browse treatments (control, dormant, and summer)

	Browsing treatment		
	Control	Dormant	Summer
HT (cm)	35%	34%	13%
RCD (mm)	55%	55%	34%
RV (cm ³)	207%	192%	82%
FOLR	170%	144%	41%
SDW (g)	93%	96%	38%
TRDW (g)	21%	75%	21%
LRDW (g)	445%	213%	78%
R:SDW	-15%	-31%	-33%
STNC (mg)	175%	145%	83%
TRTNC (mg)	34%	9%	-20%
LRTNC (mg)	653%	200%	-25%
WTTNC (mg)	85%	70%	2%

HT height, RV root volume, SDW shoot dry weight, TRDW taproot dry weight, LRDW lateral root dry weight, R:SDW root to shoot dry weight ratio, STNC total non-structural carbohydrates of shoot, TRTNC total non-structural carbohydrates of taproot, LRTNC total non-structural carbohydrates of lateral root, WTTNC total non-structural carbohydrates of whole tree

The more rapid growth rates relative to initial size and improved physiological status (i.e., higher photosynthetic rates) of container seedlings we observed did not produce significant interactions with browsing treatments. This may have been associated with the relatively well-watered conditions of this controlled greenhouse trial; responses may vary under exposure to moderate to severe drought, which represents a potential caveat when extrapolating these results to field conditions. Our second hypothesis that season of herbivory would cause variable seedling responses, however, was confirmed, but results were equally applicable across stock types. Although simulated summer browsing promoted generally higher photosynthetic rates, this was insufficient to overcome leaf area reductions. These seedlings, therefore, had lower biomass and TNC content than control or dormant-browsed seedlings. Summer-browsed seedlings showed evidence of recovery of TNC concentrations, suggesting that growth may improve the following year in the absence of additional browsing. Sustained browsing through several growing seasons, however, will further deplete TNC stores and impair seedling capacity to compete with vegetation for above- and below-ground resources, thereby reducing growth and likely increasing mortality (Canham et al. 1994; Morrissey et al. 2008). Our data helps illustrate the physiological basis for justification of browse protection of northern red oak seedlings in areas of high herbivore populations to help ensure successful regeneration.

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