TIMING TREATMENTS TO THE PHENOLOGY OF ROOT CARBOHYDRATE
RESERVES TO CONTROL WOODY INVASIVE PLANTS

A Dissertation Presented

By

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DEDICATION

To my parents, for showing me what is most important in life.

ACKNOWLEDGEMENTS

ABSTRACT

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RESERVES TO CONTROL WOODY INVASIVE PLANTS

MAY 2005

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In the Northeast, land managers are combating the deleterious effects that invasive plants have on other species and natural communities with attempts to remove them or substantially reduce their density. Control methods vary depending on the target species' growth form, the extent of the invasion, and other species and resources at the site. Mechanical treatment, prescribed fire, hand-pulling, and application of herbicides, alone or in combination, have all been used to attempt control.

Woody invasive plants are often difficult to eliminate due to their ability to sprout from stems, stumps, and roots. Successful control of these species requires understanding temporal variations in their below-ground resources. Total non-structural carbohydrate (TNC) reserves in the roots of woody species support growth following disturbance and generally follow an annual cycle of depletion and replenishment. This study evaluates the effectiveness of treatments when applied during periods of decreased TNC reserves.

Treatments were applied to seven invasive shrubs (*Cornus racemosa, Rhamnus cathartica, Rosa multiflora, Berberis thunbergii, Lonicera morrowii, Smilax rotundifolia,* and *Cytisus scoparius*) at three different sites in Massachusetts and New York. Treatments included cutting and/or burning, applied singly or in combination, in either the dormant or growing seasons.

TNC were depleted following all treatments. Dormant-season-treated plants, whether cut or burned, sprouted and replenished their reserves within the following growing season. For growing-season-treated plants TNC remained depleted longer, with a greater effect on plants that received more treatments. For most species studied, TNC recovered to pre-treatment levels by the end of one growing season without treatment.

Sprout growth was influenced by the extent of carbohydrate reserves present before treatment. Biomass and heights of sprouts were significantly lower in growing-season-treated plants than those treated in the dormant season, even when data were adjusted for different lengths of recovery time.

All treatments reduced the cover of the target invasive shrub. As the plants sprouted, they regained some of their initial cover and are expected to dominate without further treatment. Timing treatments to the cycle of TNC can increase the effectiveness of control methods, although repeated treatments may be necessary for several years.

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INTRODUCTION

Invasive woody plants are common throughout the Northeast and are spreading

from disturbed areas into native vegetation (Randall & Marinelli 1996, Hunter & Mattice

2002). Included are shrubs, trees, and vines that grow rapidly, form dense thickets, and

negatively impact native species and natural communities. Non-native invasives, such as

Asian honeysuckles (*Lonicera* spp.), Japanese barberry (*Berberis thunbergii*), autumn

olive (*Elaeagnus umbellata*), burning bush (*Euonymus alata*), multiflora rose (*Rosa

multiflora*), and European and glossy buckthorn (*Rhamnus cathartica & Rhamnus

frangula*), are considered by the Invasive Plant Council of New York State,

Massachusetts Invasive Plant Working Group, New England Wildflower Society, U.S.

Forest Service and others as some of the worst invaders in the region. Certain native

species, some planted beyond their pre-Columbian ranges, are similarly aggressive in old

fields currently valued as wildlife habitat. Examples include gray dogwood (*Cornus

racemosa*), black locust (*Robinia pseudoacacia*), catbrier (*Smilax* spp.), and false indigo

(*Amorpha fruticosa*). Land managers are interested in removing or substantially reducing

the density of these species to mitigate their negative impacts. Successful management

requires knowledge of individual species' growth-habits (including their ability to

sprout), ecological requirements, and their impacts on native species and communities.

Impacts of Invasive Species on Other Species and Communities

In the Northeast, woody invasive species have invaded a variety of habitats from grasslands (native or formerly kept open for agriculture and grazing) to wooded tracts (impacted by natural disturbances such as fire, wind, ice storms, and insect and disease outbreaks or anthropogenic disturbances such as timber harvesting and road building) to intact forests. Invasive species compete with other species directly, alter ecosystem processes, change hydrological characteristics where they invade, and, in the case of non-native species, may hybridize with native species and thereby degrade gene pools (Randall 1996). Examples of woody invaders and their impacts include non-native species such as: oriental bittersweet (*Celastrus orbiculatus*), a vine that climbs up trees and competes with them for light, water, and nutrients as well as making the trees prone to structural damage due to its weight (Weatherbee 1994, Randall & Marinelli 1996); Japanese barberry which can adversely affect soil pH (Kourtev *et al.* 1998); glossy buckthorn which invades rapidly and overtops native species (Randall & Marinelli 1996); Amur honeysuckle (*Lonicera maackii*) which is reported to negatively affect fecundity, fitness and survival of native annuals (Gould & Gorchov 2000); and native species like gray dogwood which invades old fields and grasslands changing habitat structure and composition for grassland birds including grasshopper sparrows, bob-o-links and harriers (Mitchell 2000).

Early successional ecosystems (grasslands, heathlands, and abandoned farmlands) provide important habitats for many northeastern rare species including grassland birds,

butterflies and moths, and several plants. Historically open lands are important as habitat

for game species, for their aesthetic value, and for increasing habitat diversity regionally.

Fields have been kept open by mowing and grazing since Colonial times. Before that,

Native Americans burned fields to keep them open (Olson 1978, Stevens 1996), and this

practice was continued by European settlers in the Northeast. Shifts in agriculture to the

Midwest, increased effectiveness of fire suppression efforts, and increased concern over

the effects of open burning on air quality have resulted in increased opportunities for

woody species to invade grasslands and old fields. In some areas woody invasives, such

as gray dogwood, multiflora rose, and autumn olive have converted open grasslands into

shrub thickets threatening or eliminating grassland obligate species (Dunwiddie *et al.*

1997, Mitchell 2000). In other cases, woody invasive species have spread into naturally

wooded tracts resulting in decreased regeneration of native species (Clark & Mattrick

1998, Clark *et al.* 1998).

Invasive species can affect natural communities by decreasing species richness

and altering ecosystem processes. Woody species, including trees and shrubs, can alter

understory richness and seedling establishment by decreasing the amount of light

available in the understory, reducing water and/or nutrients available in surface soils, and

in some cases producing allelopathic compounds (Woods 1993, Myers & Bazely 2003).

Ecosystem processes such as nutrient cycling and frequency and intensity of natural

disturbances can also be impacted by invasive species (Rice *et al.* 2004). Kourtev *et al.*

(1998) suggest that invasions by two species, Japanese barberry and Japanese wiregrass

(*Microstegium vimineum*), altered soil pH and caused a reduction in the thickness of litter

and organic horizons. These effects, separate from the increased shading of the understory, could impact native species in the invaded habitats.

Characteristics of Woody Invasive Species

The most aggressive invasive species have a suite of characteristics that allow them to rapidly invade and dominate suitable habitats. These traits include prolific seed production and seedling survival, rapid growth rate, ability to spread asexually, and ability to survive in a wide range of habitats (Myers & Bazely 2003). Many non-native invasive species were introduced to North America because they had one or more of these characteristics. Multiflora rose was introduced for erosion control and for living fences, because it grows rapidly and is not readily eaten by livestock due to its sharp thorns (Clark *et al.* 1998, Epstein & Hill 1999). Autumn olive was recommended for roadside plantings because of its ability to grow rapidly in disturbed soils, tolerance of salt, and ability to fix atmospheric nitrogen (Dirr 1990, Randall & Marinelli 1996). Asian shrub honeysuckles produce abundant fruit (readily dispersed by birds and other wildlife) and were planted across the region for erosion control and wildlife cover (Clark *et al.* 1998). These and other shrubs planted as hedgerows, for erosion control, or as "wildlife plantings" have invaded grasslands, abandoned fields, and nearby forests and wetlands.

The reproductive strategies of invaders often result in successful dispersal and establishment. Large amounts of seed are often produced as a consequence of having a

long period of flower and fruit production as in common and glossy buckthorns. These species produce fruits throughout much of the growing season (Mehrhoff 1998). Other species, e.g. Norway maple (*Acer platanoides*) and burning bush, are successful because of high germination rates and successful seedling establishment (Clark *et al*. 1998, Webb & Kaunzinger 1993). Rapid growth and maturation of some woody invasives result in their populations expanding rapidly once established at a site. In addition, many of the most problematic woody species in the Northeast can spread vegetatively as well as by seed.

Rapid growth rates, absence of natural diseases or insect pests, and ability to grow in a wide range of habitats have contributed to the spread of invasive species. Ellsworth *et al*. (2004) note that oriental bittersweet vines can grow > 4 meters in 12 weeks in full or partial sun. For this vine, rapid growth allows the plant to overtop taller vegetation and thereby gain access to additional resources. Many invasive species can tolerate a variety of environmental conditions. For example, common and glossy buckthorns are found in shade and full sun, wet and dry soils, and in a variety of soil types (although they prefer neutral or alkaline soils, Clark & Mattrick 1998). This ability to occupy a range of sites means that dispersed seed is more likely to find suitable germination conditions than seed of species that require a narrower range of seedbed conditions. Vegetative reproduction also allows many invasive species to quickly spread once established and persist following disturbance. Woody species, in particular, can sprout from damaged stems or roots with increased stem density following disturbance. Stored

carbohydrate reserves provide the energy necessary for this growth; the more reserves, the more vigorously a plant can recover.

Carbohydrate Reserves and Their Role in the Growth and Persistence of Woody Species

Carbohydrates, including sugars, alcohols, starch, and other compounds, are products of photosynthesis and are variously used and stored by plants. Simple carbohydrates are created during photosynthesis in leaves (and in some cases stems and other tissues), synthesized into more complex compounds, and exported from the site of fixation to carbohydrate sinks throughout the plant. These sinks vary according to the needs of the plant for growth, reproduction, defense, and respiration. Carbohydrates are used for building cell walls and in the synthesis of fats, proteins, and other molecules as needed. Excess carbohydrates are stored (primarily as sugars, alcohols, and starch) for later use and can be converted into soluble compounds for transport to other sinks when necessary.

The forms of carbohydrate stored vary among plant species, storage tissue, and time of the year (Cook 1966, Kozlowski & Pallardy 1997). Starch is one of the most common storage carbohydrates and is readily converted to soluble sugars when needed for growth (Cook 1966, Loescher *et al.* 1990). Total nonstructural (available) carbohydrates (TNC) include reducing sugars (glucose, fructose), non-reducing sugars (sucrose), fructosans, dextrins, and starch. Two organs store the majority of reserve carbohydrates: stems and coarse roots (Cook 1966, Kozlowski 1971, Kozlowski 1992);

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but reserves can also be present in fine roots, foliage, fruits, and buds. In general reserve carbohydrates are stored as starch in roots, but as sucrose in stems.

One of the main uses of reserves is to support growth and respiration prior to leaf-out (and subsequent production of photosynthate) as well as after disturbance such as herbivory or fire (Cook 1966, Loescher *et al*. 1990, Kozlowski 1992, Rodgers *et al*. 1995, Sakai *et al*. 1997). Depending on the species, one-half to two-thirds of stored reserves can be used to support growth (Kozlowski 1992). Reserves are also important for flowering, fruiting, and seed maturation. Reserves along with current photosynthate are used for the growth of reproductive structures including flowers and fruits (Oliveira & Priestley 1988). In woody species, below-ground reserves support sprouting following severe disturbances that kill or eliminate above-ground tissues, whereas reserves in stems often can support new growth following less severe disturbances such as defoliation. Reserves are also used in the production of defensive chemicals important in the prevention of invasion by plant pathogens and insects (Mooney *et al*. 1983). The reduced capacity of stressed trees to withstand attacks is correlated with low carbohydrate reserves (Christiansen *et al*. 1987, Waring 1987). In general the lower the reserves, the less likely a plant will survive disturbance or other stresses (Gregory *et al*. 1986).

Carbohydrate reserves vary seasonally. In the temperate Northeast, reserves are normally depleted during budbreak and subsequent growth in the spring, replenished during the growing season, and gradually used in respiration during the dormant season (Donart 1969, Kramer & Kozlowski 1979, Gregory *et al*. 1986, Loescher *et al*. 1990,

Johansson 1993, Droege 1996). Reserves are shifted from roots to shoots in anticipation

of leaf-out. During the early stages of shoot expansion in deciduous trees, carbohydrate

reserves provide the energy and compounds necessary for shoot and leaf expansion.

Once the newly expanded leaves begin to photosynthesize, carbohydrates are produced

which are used first for continuing leaf growth, then for growth of other tissues, and

finally for accumulated reserves (Kozlowski 1971). Carbohydrates are not exported to

storage tissues until leaves are fully mature. Species which have one or more additional

growth flushes have multiple depletion and replenishment cycles within a single growing

season (Mooney *et al*. 1983, Birk & Matson 1986). Annual reserve minimums generally

occur during early vegetative growth, but in some instances minimums may occur during

flowering or secondary growth (Cook 1966). The rate of use and replenishment depends

not only on the species, but also on factors such as site fertility, climate (especially

temperature and precipitation), and disturbance (Ritchie 1982, Birk & Matson 1986).

Although studies of reserve carbohydrates often focus on the percentage of

carbohydrates in various plant tissues, the total amount of stored reserves in a plant

depends on the overall biomass of stems, roots, and leaves. Root and stem bark often

have higher concentrations of reserves, but the total amount is comparatively small

relative to stores in the wood (Kozlowski 1992). In *Fagus sylvatica*, although the

concentration of carbohydrates was higher in stem bark than in wood, about 80% of the

carbohydrate pool was in the wood and only 18% in the bark (Kozlowski 1992). Roots

(bark and wood) generally have higher concentrations of carbohydrates than stems. The

fraction of the total carbohydrate pool located in the root system varies with the age of

the plant as root-to-shoot ratios change. A large tree will have more of its total

carbohydrate pool in the above-ground tissues (i.e. stems, branches, and leaves) than in

the root system, as above-ground tissues are a far greater proportion of the dry weight of

the tree (Birk & Matson 1986). Generally, reserves are depleted from above-ground

tissues for stem, leaf, and reproductive growth, whereas those stored in roots are used

both above- and below-ground.

The amount of reserves varies between plants with different reproductive

strategies. Annual plants transfer far fewer carbohydrates to roots than perennial plants

(Trlica & Singh 1979), as their carbohydrates generally are used to produce seed. Plants

that resprout following disturbance generally have larger storage roots and more reserves

than those that rely more on seed production (Pate *et al*. 1990, Bowen & Pate 1993).

Resprouters also have lower growth rates than their congeners indicating that the storage

of resources may be at the expense of growth (Pate *et al*. 1990, Bowen & Pate 1993,

Sakai *et al.* 1997, Bell & Ojeda 1999).

Disturbances including drought, defoliation, or stem death can reduce the amount

of reserves accumulated during a growing season (Loescher *et al.* 1990). The amount of

stored reserves can impact the health and recovery of plants following disturbance. The

more reserves, the better an individual will be able to survive stress; whereas depleted

reserves can result in plant death (Gregory & Wargo 1986, Kozlowski 1992). The timing

and frequency of disturbances also affects the amount and recovery of reserves. Cook

(1966) and McConnell and Garrison (1966) report that for woody plants stem elongation

and rate of growth in the spring are proportional to the amount of carbohydrate reserves, and that the timing of removal of above-ground biomass during the natural cycle of TNC depletion and recovery affects the success of regrowth. Since this early work, many researchers have investigated the effects of frequency, timing, and extent of defoliation on carbohydrate reserves of a variety of trees and shrubs (FitzGerald & Hoddinott 1983, Gregory & Wargo 1986, Kays & Canham 1991, Renaud & Mauffette 1991, Erdmann *et al.* 1993). Removal during the winter dormant season will have less impact on regrowth than removal during the growing season when reserves are reduced (Kays & Canham 1991, Johansson 1993). Late-season defoliation can cause a decrease in carbohydrate reserves (due to resprouting) which can impact the vigor of the individual at the beginning of the following growing season (Gregory & Wargo 1986, Loescher *et al.* 1990).

Treatments to Reduce Woody Plant Invasion

Eradicating woody invasive species may involve a variety of management techniques including cutting and removal of above-ground biomass, prescribed burning, and application of herbicides (Randall & Marinelli 1996). These techniques are often used in combination, and it is usually necessary to repeat them in order to achieve some reduction in the abundance of the undesirable vegetation (Rice 2004). For woody species, timing of the application is more important than the control method used. Although often ineffective, dormant-season mowing and burning are still recommended for reducing shrub cover in northeastern grasslands (Jones & Vickery 1997). Both

treatments remove above-ground biomass but have minimal lasting impact on woody invasive species due to their ability to re-sprout from stumps and/or underground roots and rhizomes. Herbicides are effective when applied in conjunction with mechanical treatments and/or when applied to individual plants, but depending on the method of delivery may be inappropriate or inefficient for use in some situations (e.g. in watersheds protecting drinking water supplies, and in natural areas supporting rare plant species that might be adversely impacted by broadcast sprays). Prescribed fire is often considered for controlling non-native invasive plants (Rice 2004), and although it may be useful in controlling some species, it is not appropriate in all situations. As with any disturbance, fire (especially during the dormant season) may increase the presence of exotics by creating conditions that allow invasion or stimulate vegetative regrowth. Fire can aid in germination of banked seeds, create scarified soil appropriate for germination of newly dispersed seeds, and alter soil chemistry to the benefit of some exotic species (Haskins & Gehring 2004).

Objectives

Although land managers have used fire and mechanical treatments to control woody invasive species, little work has documented the effects of treatments on root carbohydrate reserves, sprout production, and impacts on non-target species. Because reserves are used to produce new sprouts, we need to know when reserves are at their lowest and how carefully timed treatments can further deplete them. The objective of this research was to document seasonal cycles in reserve carbohydrates of woody

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invasive plants to evaluate the ability of these plants to recover reserves and above-ground biomass following mechanical and prescribed fire treatments, and to determine if non-target species cover increased once the invasive was controlled. I chose seven species that occurred among three different habitat types to provide both species- and site-specific data to identify broader trends of how woody invasive species respond to cut and burn treatments. I included two native (*Cornus racemosa* and *Smilax rotundifolia*) and five non-native species (*Rhamnus cathartica*, *Rosa multiflora*, *Berberis thunbergii*, *Lonicera morrowii*, and *Cytisus scoparius*) that encompass seven different families, a variety of growth forms, and occur in different habitat types. Cut and/or burn treatments were applied during the dormant and/or growing seasons to determine in which season treatments should be applied to achieve lasting control.

Chapter Two provides a review of current knowledge about the seven species I studied as well as descriptions of the study sites. In Chapter Three I describe the seasonal variation of total non-structural carbohydrates in the roots of six of these species and the influence of short-term drought on the recovery of reserves (I did not evaluate carbohydrates in *Cytisus* as it did not readily resprout). Chapter Four evaluates the effects of growing- and dormant-season treatments (cutting or burning) on reserve carbohydrate levels and the implications for management protocols. This is followed by an analysis of the above-ground response of the six species following treatments (Chapter Five). Chapter Six reports the influence of treatments to control all seven invasive species on the composition and abundance of native species.

Chapter Seven summarizes the results of this study and discusses how managers can use the broad-scale and species-specific information provided when planning and executing invasive species control efforts.

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CHAPTER 2

SITE AND SPECIES DESCRIPTIONS

To provide species-specific information to land managers throughout the region, I studied several woody invasive species at three locations representing very different site conditions. The seven species include native and non-native taxa, all of which are considered invasive at the study locations. Following are descriptions of the species (along with control methods suggested by others prior to this study) and sites that were included in the study. Nomenclature follows Gleason and Cronquist (1991).

Species Descriptions

Cornus racemosa

Gray dogwood (*Cornus racemosa* Lam.) is a medium-sized shrub (1-5 m tall) that often forms dense thickets in open habitats (Gleason & Cronquist 1991, Boeken & Canham 1995). Although it produces abundant fruit that is dispersed by birds, once established it primarily spreads vegetatively. New shoots (suckers) form on an extensive root network resulting in dense clones that often have distinct margins (Boeken & Canham 1995). It occurs in moist-to-wet habitats, and although native to the Northeast it has become invasive in old-fields of New York State. Boeken and Canham (1995) report

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that it is the most abundant shrub in old-fields in the Hudson Valley. Where dense

thickets occur, it can effectively prevent establishment of tree seedlings, so it has been

suggested as a possible beneficial planting for power line rights-of-way or other areas

where it is desirable to arrest succession to a forest community (Pound & Egler 1953,

Niering & Goodwin 1974, Boeken & Canham 1995). Although individual stems have a

lifespan of only 10-20 years, surrounding stems in a thicket can quickly take advantage of

the light and space relinquished as a stem dies, so the thicket in general maintains a near

constant stem density and appearance (Boeken & Canham 1995).

Maintaining old fields as grassland bird habitat requires preventing woody species

from dominating. Prescribed fire and mowing activities during the dormant season have

had limited success in controlling dogwood invasion, although recent attempts using

growing season treatments have had some success (Mitchell 2000). Dogwood clones can

survive unless the entire clone is treated.

Rhamnus cathartica

Common buckthorn (*Rhamnus cathartica* L.) is a small tree 6-8 m tall, native to

Europe and Asia, and naturalized in the eastern U.S. since its introduction as a hedge and

for wildlife habitat during the 19th century (Clark & Mattrick 1998). Although common

buckthorn prefers upland sites, it grows well in both wet and dry habitats. It is tolerant of

dense shade, and flowers and fruits all season long (Weatherbee *et al.* 1998). Individual

plants are easily overlooked as they do not possess showy flowers or fruits. They are,

however, conspicuous in the early spring and late fall, as they leaf out earlier and hold their leaves longer than native species (Harrington *et al.* 1989, Archibold *et al.* 1997). This longer growing season may give them a competitive advantage over native species (Harrington *et al.* 1989, Clark & Mattrick 1998). Although buckthorn fruits are cathartic, they are still eaten by birds and wildlife and thereby dispersed across the landscape. Archibold *et al.* (1997) studied age distribution, fruit fall, germination, allelopathic effects, and potential control methods for buckthorn at several sites near Saskatoon, Saskatchewan, Canada. The amount of seed produced, its long leaf lifespan, its ability to stump sprout, and potential allelopathy make this species an aggressive competitor that displaces native species. Seed rain was calculated as 620 viable seeds per square meter in the surface 10 cm of soil beneath a buckthorn stand. Control efforts have included hand-pulling smaller plants and cutting followed by herbicide application to stumps. Fire has also been tested as a control method, although it may only be effective at killing seedlings. Sprouting from stumps occurs with all treatments (cutting, burning, and herbicide application), although direct application of herbicides to cut stumps was successful in preventing up to 90% of stumps from sprouting. Little is known regarding the longevity of the seed bank.

Rosa multiflora

Multiflora rose (*Rosa multiflora* Thunb.) has a growth form which produces a shape similar to a fountain with long, slender recurving branches (Dirr 1990) which may climb neighboring vegetation. It can grow 1-3 m high with a spread of 3-5 m, has a high

growth rate, can form new ramets by layering (Lehman 1999), and sprouts from the root

collar or low stems. Multiflora rose is native to Japan and Korea and escaped from

cultivation in the U.S. after its introduction in 1868. Originally promoted by the U.S.

Department of Agriculture as a living fence, it was distributed to farmers for this purpose

(Weatherbee 1994, Epstein & Hill 1999). Birds disperse its fruits into pastures, open

woods, and even undisturbed areas. Due to its thorny branches, multiflora rose is not

browsed and therefore spreads rapidly once established. Control using repeated cutting

and herbicide application has worked in some areas (Randall & Marinelli 1996), although

the most promising long-term control method may be rose rosette disease (RRD). This

natural, mite-transmitted disease is lethal to multiflora rose and is spreading east from the

Midwest where it has significantly reduced rose populations (Amrine *et al.* 1990). RRD

currently occurs in 16 states south and west of New York and New England (Lehman

1999, Hong *et al.* 2002, Hartzler 2003).

Berberis thunbergii

Japanese barberry (*Berberis thunbergii* DC.) is a dense, spiney shrub of rounded

form that is usually broader than tall at maturity. Individuals may be nearly 3 m tall,

although 1-2 m are more common, with widths of 1-2.5 m (Dirr 1990, Gleason &

Cronquist 1991). It is one of the first shrubs to leaf-out in the spring and flowers in

April-May. Native to Japan, it was introduced to the United States in 1875 as an

ornamental. Dirr (1990) lists 29 cultivars. It has invaded pastures, woodlands, ledges,

and floodplains (Weatherbee *et al.* 1998, Silander & Klepeis 1999). In the Northeast it

was likely not naturalized until 1910, after it gained popularity as an alternative for its congener common barberry (*B. vulgaris*), which is an alternate host for wheat rust (Silander & Klepeis 1999). With its ability to survive under a wide range of soil (it prefers basic but can grow in moderately acid soils) and light conditions, it has successfully invaded relatively undisturbed forests of the Northeast (Cassidy *et al.* 2004). Kourtev *et al.* (1998) report that soil pH under *Berberis* was significantly higher than in uninvaded soils, although Cassidy (2002) found that *Berberis* growth was not affected by soil pH. It has high concentrations of alkaloids that make it unpalatable to deer, which may contribute to its ability to form dense monospecific stands (Kourtev *et al.* 1998). Japanese barberry produces abundant berries eaten by a variety of bird species (Silander & Klepeis 1999). This may aid in long distance dispersal, but Silander and Klepeis (1999) found that the majority of seedlings occur beneath or within 1m of the canopy of a barberry shrub. Sprouting from stems, root collars, and possibly rhizomes with or without disturbance leads to high stem turn-over (Ehrenfeld 1999, Silander & Klepeis 1999). As with several other invasive exotic shrubs, Japanese barberry has an extended growing season relative to native plants allowing it to take advantage of available light prior to canopy leaf-out and following leaf senescence (Silander & Klepeis 1999). Japanese barberry has been controlled by hand-pulling or digging, herbicide application to sprouts after cutting or to foliage in the spring before native species leaf-out, and prescribed fire (Randall & Marinelli 1996, Silander & Klepeis 1999).

Lonicera morrowii

Morrow's honeysuckle (*Lonicera morrowii* A. Gray) is one of several introduced Asian honeysuckles. Many honeysuckles and their cultivars (nearly 180) occur in the United States including several native species. Most non-native honeysuckles, including several varieties and forms, were introduced in the late 1700s through the 1800s. The most problematic (*Lonicera maackii*, *L. morrowii*, *L. tatarica*, *L. xylosteum*, *L.* x bella) are 2-4 m tall shrubs that form dense thickets shading out ferns, grasses, and wildflowers (Clark *et al.* 1998). Honeysuckles were once promoted by the U.S. Soil Conservation Service for erosion control and wildlife cover (Clark *et al.* 1998). In North America these species are easy to culture and propagate and are generally free from detrimental insects and diseases, which make them well suited for landscaping. Unfortunately, these characteristics also allow them to become noxious weeds that readily invade areas of natural vegetation. Honeysuckles produce large quantities of berries which are eaten by birds resulting in the spread of seeds into uninvaded areas, particularly young forests and floodplains (Weatherbee *et al.* 1998). They readily sprout from stumps following disturbance and stems lying on the ground. The hybrid *L. x bella* has a longer growing season than the native species with which it co-occurs (Harrington *et al.* 1989), and its increased leaf longevity may give it a competitive advantage over native species. Combined estimates of carbon gain due to early leaf-out and late senescence for *L. x bella* growing in the understory indicate that 50% or more of the annual carbon gain for the plant may occur during periods when native species are leafless (Harrington *et al.* 1989).

A study of competition between *L. tatarica* and native species demonstrated that herb richness and cover as well as tree seedling density decline with increasing cover of the exotic shrub (Woods 1993). Gould and Gorchov (2000) found that *L. maackii* can reduce the fecundity and survival of annual herbs, although the mechanism by which it does so is not clear (possibly competition for light or other resources, or allelopathy). As with other woody invasives, hand pulling and cutting followed by herbicide application to the stumps have been successful in managing some populations (Randall & Marinelli 1996).

Smilax rotundifolia

Catbrier (*Smilax rotundifolia* L.) is a native woody vine that has become locally invasive in coastal New York and New England. It uses tendrils to climb 3-6 m covering shrubs and small trees, eventually shading out anything below and in some cases breaking branches due to its weight. Fike and Niering (1999) report that dense *Smilax* thickets have prevented tree development and establishment at several sites in Connecticut. It has deciduous leathery leaves and green stems that arise from slender, rhizomatous roots near the soil surface. It spreads by seeds and sprouting from the roots. Individual stems live 2-to-4 years and upon dying contribute to catbrier's flammability as they may remain entwined with live stems above the surface before they break and fall to the ground (Ohman 2005 expected). Catbrier is highly flammable and acts as a ladder fuel (bringing fire into the canopy) increasing the intensity and spread of fire. Carey (1994) reports that catbrier is resistant to most herbicides, but an ongoing study on

Naushon Island suggests that catbrier is killed by glyphosate-based herbicides (Polatin, pers. comm.).

Cytisus scoparius

Scotch broom (*Cytisus scoparius* [L.] Link.) is native to Europe and was planted in New England before 1920. It occurs from Nova Scotia west to New York, and south to Georgia with several populations in New England. It also occurs in the Pacific Northwest and central California where it is a particular problem in rangelands. A leguminous shrub, it can form dense thickets more than 2 m tall. Individual plants generally live for approximately 20 years (Bossard & Rejmanek 1994, Downey & Smith 2000, Smith 2000). Scotch broom produces prolific, long-lived seeds, which can be sent up to 5 m from the parent plant when the mature seed pods burst open. There is also evidence of ant dispersal (Smith 2000). Once established, Scotch broom spreads rapidly and forms large thickets that displace native vegetation and possibly affect animal distributions (Smith 2000). Young twigs of Scotch broom (which make up approximately 25% of its above-ground biomass) are green and contribute to its positive carbon gain throughout the year through stem photosynthesis (Bossard & Rejmanek 1992, Nilsen *et al.* 1993, Smith 2000). Scotch broom is highly flammable and can increase fire intensity. Mature plants can sprout from the root crown after a disturbance (i.e. fire or cutting) that injures or kills above-ground stems. Seed germination is high following disturbances that expose mineral soil. Seed banks have been measured in the range of 190 to 50,000 seeds m^{-2} in Australia (Smith 2000, Parker 2001). Although fire

can reduce the seed bank by up to 80% (Downey 2000), seeds that remain are usually sufficient to regenerate a stand. Control efforts require initial removal or killing of above-ground stems, followed by treatments of the resulting seedlings before they are reproductively mature (Downey & Smith 2000). Biocontrol agents are also being evaluated to control Scotch broom (Bossard & Rejmanek 1994, Harman 1999).

Study Sites

Each of the above-mentioned shrub species was studied at one of three locations: Montezuma National Wildlife Refuge - Seneca Falls, NY; The Nature Conservancy's preserves in Sheffield, MA; or Naushon Island – Gosnold, MA (Figure 2-1). Following are descriptions of each of the study locations.
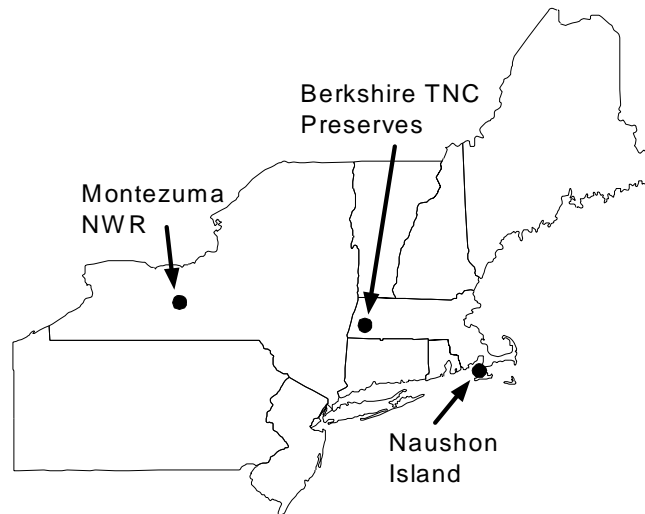
Figure 2-1. Locations of study sites across the northeastern United States.

Montezuma National Wildlife Refuge

Montezuma National Wildlife Refuge is located in Seneca Falls, Tyre, and Montezuma in Cayuga, Wayne, and Seneca Counties in the Finger Lakes Region of central New York. The refuge is primarily managed as habitat for migratory birds – both waterfowl and upland grassland species. Its 2,860 hectares are located in a matrix of agricultural land and provide habitat features not available in highly managed agricultural fields. Soils are moderately well- to somewhat poorly-drained silt loams in the Cazenovia and Ovid series (Hutton 1972). The humid continental climate is moderated by the effects of the Finger Lakes and Lake Ontario, which retards warming in the spring and delays cooling in the fall. The average growing season is approximately 185 days for the Finger Lakes region with an average annual precipitation of 99 cm.

Many of the open grasslands on the refuge are rapidly succeeding to shrublands and forests. Refuge managers use a variety of techniques including prescribed fire and mowing to retard or reverse succession at key sites. I worked at two of these: the Lay Road field (near the Esker Brook Trail) and the Clark Ridge field (off of Wood Marsh Road) (Figure 2-2). The Lay Road field has been managed with a mixture of mowing and some prescribed fire on a two- to three-year rotation for at least ten years (Mitchell 2000) but had abundant shrubs and small trees at the beginning on this project. The field was dominated by 1.5-2 m tall gray dogwood, grasses and goldenrods (*Solidago* spp.). Other shrubs included common buckthorn, blackberry (*Rubus allegheniensis*), red-osier dogwood (*Cornus sericea*), and honeysuckle. Poison ivy (*Toxicodendron radicans*) and

black swallowwort (*Vincetoxicum nigrum*) are common. The Clark Ridge field is similar to the Lay Road site, although the gray dogwood and other shrubs are taller at 2-3 m. Other shrubs and trees found at this site include common buckthorn, blackberry, multiflora rose, and some small white ash (*Fraxinus americana*).
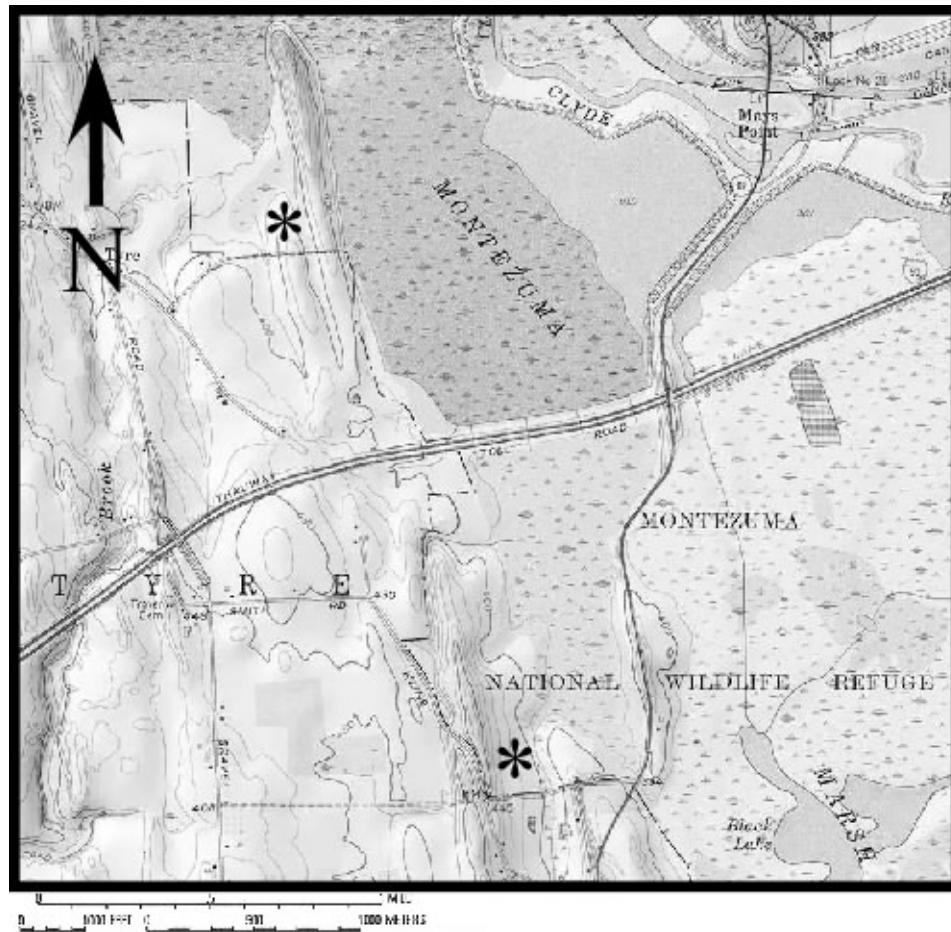
Figure 2-2. Locations of study sites (*) at Montezuma National Wildlife Refuge. Clark Ridge is north of the NY State Thruway (bisecting the figure) and Lay Road is to the south.

Berkshire Nature Conservancy Preserves

The Berkshire region of western Massachusetts, with its calcium-rich bedrock and waters, harbors one of the largest concentrations of rare species and unique natural communities in the Commonwealth. The region includes the Berkshire Hills (an extension of the Green Mountains of neighboring Vermont) as well as the Taconic Mountains (along the western border of Massachusetts). The region has a compressed growing season of approximately 130 days due in large part to its topography. Annual rainfall averages 118 cm and is evenly distributed throughout the year. Recognizing the importance of the area, The Nature Conservancy has been protecting land in Sheffield and neighboring towns and currently owns and manages more than 5,000 acres.

I established two study sites on two separate parcels owned by The Nature Conservancy (Figure 2-3). The first - the Bartholomew tract - is a mature deciduous forest dominated by sugar maple (*Acer saccharum*), black birch (*Betula lenta*), and white ash. The understory is dominated by Japanese barberry, in some cases with more than 80% cover. Soils at this site are deep, well-drained, extremely stony Nellis loams (USDA 1988). Water capacity is high and the soil is slightly acid to neutral at the surface and moderately alkaline below. Stone walls that bisect the site suggest that the land may have been pastured in the early 1900's. More recently the site had been used as a woodlot as part of a larger farmstead. Agricultural fields still exist nearby, although most are hayfields. Prior to Conservancy ownership, the land was owned by a local family that maintained a mix of fields, pastures, and woodlands.
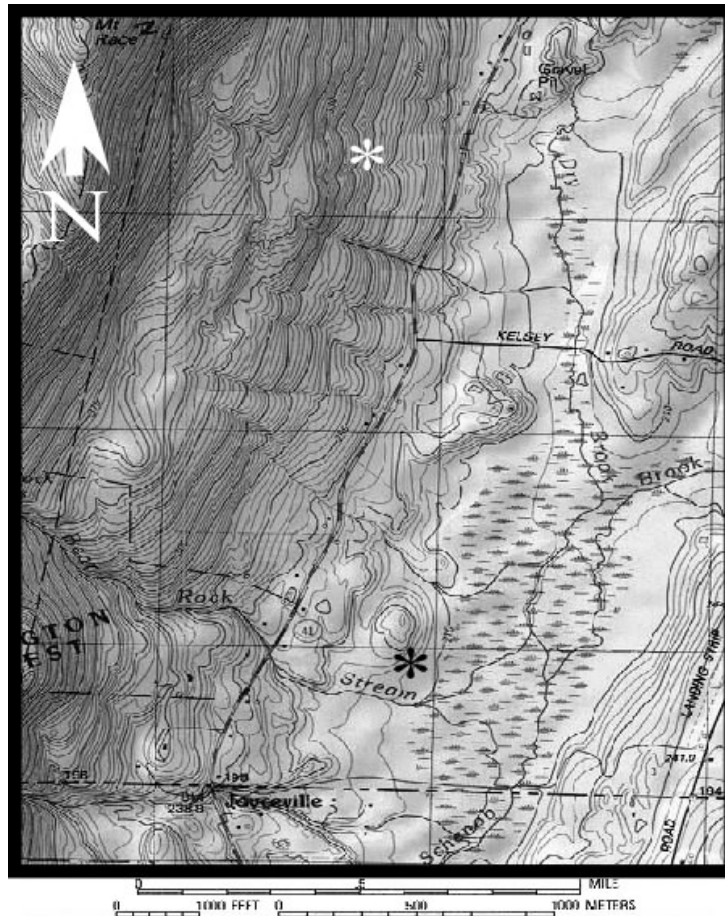
Figure 2-3. Locations of two study sites (*) owned by The Nature Conservancy in Sheffield, Massachusetts with the Bartholomew site to the north.

The second site, the Bear Rock Stream tract, is a forested swamp dominated by white ash and red maple (*Acer rubrum*). Soils are very deep, poorly-to-moderately well-drained Halsey and Hero loams (USDA 1988). The soils are neutral to alkaline and saturated during seasonal high water. There is a dense shrub understory dominated by Morrow's honeysuckle. Japanese barberry, multiflora rose, dogwood (*C. racemosa & C. amomum*), and winterberry (*Ilex verticillata*) are common. The site is approximately 8.6 km from the Bartholomew tract and is at the base of a long slope. Generally considered a wetland, it is, however, dry enough to support facultative and obligate upland trees.

Remnants of old fence lines demonstrate that this land was also used for grazing. A small town cemetery with graves dating to the Revolutionary War is located less than 100 meters from the research plots.

The Nature Conservancy manages its lands in Berkshire County for biodiversity conservation, and preserve managers started an intensive program to eradicate non-native species at the Bartholomew site in 2003. The Conservancy is interested in utilizing fire where practical to control invasive species and/or to maintain habitat structure.

Naushon Island

The Protected Field is located in the north-central portion of Naushon Island south of Woods Hole on Cape Cod, Massachusetts (Figure 2-4). Soils on the island formed from moraine deposits and are generally deep, excessively-drained Eastchop sands or loamy sands (USDA 1986). The climate is moderated by maritime influences resulting in a growing season of approximately 185 days, with annual precipitation of 117 cm. The island supported a flock of 1000-2000 sheep as well as other domestic grazers through the 1940s (Schroeder 2002). As the use of the island shifted to more recreation and less agriculture during the middle of the 20th century, formerly open pastureland was overgrown by woody vegetation. Sandy soils of the Protected Field currently support a maritime grassland community invaded by huckleberry (*Gaylussacia baccata*), catbrier and the non-native shrub Scotch broom. Where these species occur, they often dominate with nearly 100% cover. Scotch broom was introduced to the island in the late 1800s or early 1900s to stabilize exposed sand patches and reduce erosion and was well

established by the 1920s (Fogg 1930). Catbrier is a native species, but has invaded fields since the abandonment of grazing on the island and now forms impenetrable thickets across most unwooded areas. Where it occurs in near monocultures, catbrier reduces species diversity (Schroeder 2002). Both species burn intensely, even when green, and thus threaten human resources on the island. Naushon Island is privately owned, and land managers are interested in managing vegetation to support important natural communities (such as sandplain grassland) and to reduce fire hazard.
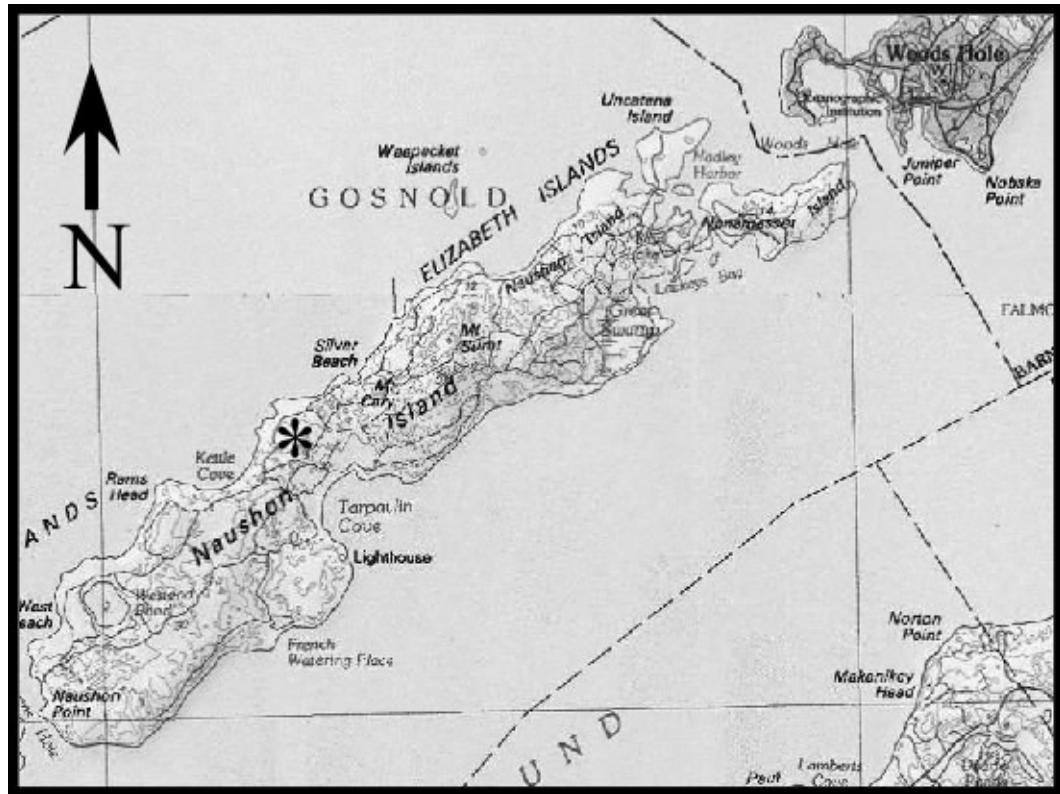
Figure 2-4. Location of the Protected Field (*) on Naushon Island, Gosnold, Massachusetts.

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CHAPTER 3

PHENOLOGY OF TOTAL NON-STRUCTURAL CARBOHYDRATES FOR SIX

INVASIVE WOODY SPECIES

<u>Introduction</u>

Carbohydrate reserves are accumulated in a variety of plant tissues for later use in

respiration, growth, and synthesis of plant compounds (e.g. defensive chemicals,

enzymes). These reserves are formed when excess photosynthate is produced and used

when current photosynthesis cannot meet the needs of the plant. Reserves are stored

throughout the plant including in leaves, stems, bark, and roots, with the majority being

stored in stems and coarse roots (Cook 1966, Kozlowski 1992). Stored carbohydrates are

used to support leaf-out in temperate deciduous species and can also be used for

flowering, fruiting, seed maturation, growth of stems, and formation of buds. Reserves

also contribute to the successful survival of a plant following disturbances such as

herbivory or fire (Cook 1966, Loescher *et al.* 1990, Kozlowski 1992, Rodgers *et al.* 1995,

Sakai *et al.* 1997).

In temperate regions, carbohydrate reserves vary seasonally, normally being

depleted during budbreak and subsequent growth in the spring, replenished during the

growing season, and gradually used for respiration during the dormant season (Figure 3-

1; Donart 1969, Kramer & Kozlowski 1979, Loescher *et al.* 1990, Johansson 1993,

37

Droege 1996). Nearly one-half to two-thirds of stored reserves are used to support

growth (Kozlowski 1992). Although depletion of reserves can occur quickly as stems

elongate and leaves expand in the spring, replenishment is generally more gradual. The

timing and pattern of depletion and replenishment vary between species and sites.

Species that have more than one flush of growth experience carbohydrate depletions with

each growth flush followed by replenishment prior to the next flush (Birk & Matson

1986). Depletion of reserves may also occur during flowering or secondary growth in the

fall (Cook 1966).
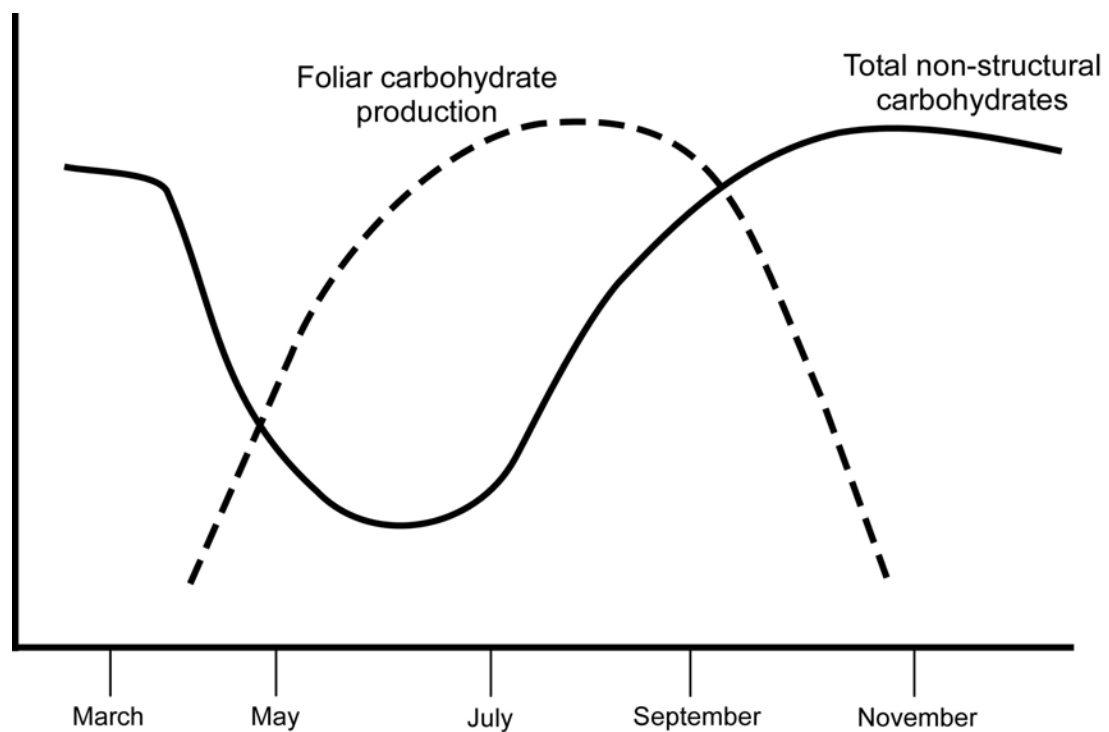
Figure 3-1. Seasonal variation of total non-structural carbohydrate concentrations in roots relative to foliar carbohydrate production.

Environmental factors like temperature, precipitation, and soil characteristics influence the use and storage of carbohydrate reserves. In some cases, reserves can be higher during drought, presumably due to a slowing of above-ground growth while photosynthetic rates are not impacted (Cook 1966). In other situations drought results in decreased reserves, which, when combined with grazing, lower the resistance of certain grass species to injury due to water stress (Cook 1966). Wan & Sosebee (1990) report that the extent and timing of water stress can have differing impacts on root growth and carbohydrate reserves including an increase of reserves at the expense of flowering, an increase in root growth (to increase water uptake), or a decrease in reserves due to a decrease in photosynthesis.

I followed the depletion and replenishment of carbohydrate reserves (total non-structural carbohydrates or TNC) in six woody invasive species in Massachusetts and New York from the spring of 2001 through the fall of 2002. Variability in TNC between the two years was compared to patterns in precipitation to determine if carbohydrate reserves declined during periods of drought. Knowledge of the timing of TNC depletion (whether as part of an annual cycle or due to environmental stress) can advise land managers interested in controlling these species, as TNC influence vigor of sprouts following removal of above-ground stems (Cook 1966, Loescher *et al*. 1990, Sakai *et al*. 1997).

Methods

Six invasive shrub species (two native and four non-native) were studied at three locations (Figure 2-1). Three species (*Cornus racemosa*, *Rhamnus cathartica*, and *Rosa multiflora*) were sampled at Montezuma NWR (Seneca Falls, NY) in old fields maintained as grassland bird habitat (Figure 2-2). *Lonicera morrowii* and *Berberis thunbergii* occurred under closed canopy forests at The Nature Conservancy's preserves in Sheffield, Massachusetts (Figure 2-3). *Smilax rotundifolia* is a woody vine that currently dominates many acres of coastal grassland on Naushon Island (Gosnold, MA) where it forms dense, nearly impenetrable thickets (Figure 2-4).

A uniformly invaded 40 x 40 meter plot was established at each site for each species (except one plot that contained both *Cornus* and *Rhamnus* in New York). These untreated plots were part of a larger study evaluating the impacts of cutting and burning treatments on total non-structural carbohydrate reserves (see Chapter 4).

Root collection

Root samples were collected from four-to-six individuals per plot approximately every four weeks from March through November in 2001 and 2002. For a given sampling date root samples were collected from different plants. For species that reproduce vegetatively from roots - *Cornus* and *Smilax* - it was impossible to determine the extent of an "individual plant." To ensure that samples for these species were

independent of one another, root sections were collected from roots of stems > 3 meters apart. Except for *Rosa* and *Rhamnus*, which had too few individuals per plot, root samples were only collected once from a given stem during the study. *Rosa* individuals were sampled up to three times over the two years, whereas *Rhamnus* individuals were not sampled more than twice. Root sections approximately 1-1.5 cm in diameter and ±10 cm long were collected with hand clippers after excavating with small garden shovels and weed tools. Each sample was placed in a plastic bag in the field, put on ice and frozen until processed. In the lab roots were washed, cut, and dried at 70° C until they reached a constant weight. They were then ground in a Wiley Mill to pass a 40-mesh screen. Ground samples were stored in a freezer until processed.

Total non-structural carbohydrate analysis

The ground root material was placed in a 70° C drying oven for at least one hour prior to sampling for total non-structural carbohydrates. Ten milligrams of ground material was placed in a test tube (three replicates per root sample) along with five Units of amyloglucosidase in 4 ml of phosphate buffer, and then incubated in a 55° C water bath for 22 hours. After incubation, a 1 ml aliquot of extractant combined with Nelson's alkaline-copper reagent and Nelson's arsenomolybdate reagent were mixed and measured colormetrically at 540 nm in a spectrophotometer (Haissig & Dickson 1979, Westhafer *et al.* 1982). TNC values were calculated as grams of TNC per gram of root expressed as a percentage.

Climate characterization

Precipitation and temperature data were available from several on-line sites including the National Climatic Data Center website (NCDC 2005); the Northeast Regional Climate Center website based at Cornell University, specifically the CLIMOD (Climate Information for Management and Operational Decisions) database (NRCC 2004); and from the New York State Climate Office website - a joint venture with Cornell and NOAA (NYSC 2004). Normal precipitation values for Berkshire and Dukes Counties are available in the soil surveys for those counties (USDA 1988, 1986). Weather stations were located in Syracuse (approximately 50 kilometers from Montezuma NWR), West Otis and Pittsfield (21 & 43 km respectively from the Berkshire sites), and on Martha's Vineyard (15 km from Naushon). Although no station was close enough to capture microsite variations in either precipitation or temperature, they provided approximations for the weather at all three sites.

Results

Overall, the six species I studied followed the typical carbohydrate reserve depletion and replenishment cycles during 2001 and 2002. TNC were depleted in the early growing season and replenished as the season progressed. During 2001 maximum initial depletions occurred for all species except *Smilax* in late May (Table 3-1). Minimum TNC for *Smilax* was a month later. Minimums for 2002 were more variable among sites and species with the species at Montezuma achieving minimums several

weeks later than the previous year. March through April 2002 at Syracuse was slightly

warmer than the previous year (two-month average 4°C in 2001 and 6°C in 2002), but

May was cooler in 2002 (16°C in 2001 and 12°C in 2002). For deciduous forests, the

timing of budburst and leaf-out is primarily driven by cumulative thermal sums following

a cooling period, although thresholds for species differ (Lechowicz 1984). Both of the

species in the Berkshire, MA sites (*Berberis* & *Lonicera*) as well as the *Smilax* at

Naushon were depleted significantly earlier in 2002 with average spring temperatures in

2002 exceeding those of 2001 (Average temperature for Pittsfield, MA Mar – Apr 2°C in

2001 and 4°C in 2002, Ave. temp for Martha's Vineyard Mar – Apr 4°C in 2001 and 7°C

in 2002). The timing of maximum replenishment was much more variable between years

and among species. In 2001, maximum TNC were achieved anytime between early July

and late October, but in 2002 the maximum was several weeks to a month later for each

species.

Table 3-1. Dates of minimum and maximum total non-structural carbohydrate
concentrations during 2001 and 2002 for *Cornus racemosa*, *Rhamnus cathartica*, *Rosa
multiflora*, *Berberis thunbergii*, *Lonicera morrowii*, and *Smilax rotundifolia*. Two dates
indicate an early and late season value.

Species	2001		2002	
	Minimum	Maximum	Minimum	Maximum
Cornus	May 24	Sep 26	Jun 4	Oct 10
Rhamnus	May 24	Aug 15	Jun 4	Oct 10
Rosa	May 25	Apr 21/Sep 26	Jun 5	Mar 28/Nov 15
Berberis	May 30/Sep 19	Jul 2/Oct 24	May 3	Jul 31
Lonicera	May 31	Sep 19/Oct 24	Mar 28	Nov 10
Smilax	Jun 26	Oct 17	Apr 26/Oct 18	Mar 19/Nov 20

TNC as a percent of dry weight varied among species. *Smilax* had the lowest overall amount (with a two-year maximum of 8.3%) and only varied by 5 percent between yearly minima and maxima (Figure 3-2). The two species from the Berkshires, *Berberis* and *Lonicera*, generally had more TNC than *Smilax* with values from 4.8 to 14.8% (Figure 3-2). The amount of variation between minima and maxima for these species was also slightly larger (6.1 – 8.4 %). *Rosa* consistently had the most TNC with minimum values (approx. 13%) higher or approaching other species maximum values (7.1 – 20.2%), but its TNC varied less (7.2 & 4.1 % for 2001 & 2002 respectively, Figure 3-2). Minimum and maximum values for *Cornus* and *Rhamnus* varied more than other species with ranges between 8.6 and 13.9 % (Figure 3-2). These two species also had at least one year of the two with very low minimum values (1.3% for *Rhamnus* in 2001 and 1.8% for *Cornus* in 2002).

Recovery times following annual minima in the spring differed between species and years (Table 3-1, Figure 3-2). In general, the plants accumulated TNC through much of the growing season with maximum replenishment taking 111 – 163 days (possibly more if the maximum was not achieved prior to my last sampling). This is nearly the entire frost-free period (Table 3-2). *Berberis* required less time than the other species and recovered reserves in just one month. The other species may also be able to recover more quickly depending on climate, site, or disturbance factors, as *Smilax* also recovered its reserves in one month at the end of 2002 after experiencing nearly a whole summer of low TNC values and *Rhamnus* recovered in 83 days during 2001, a dry year at Montezuma NWR (Table 3-3).
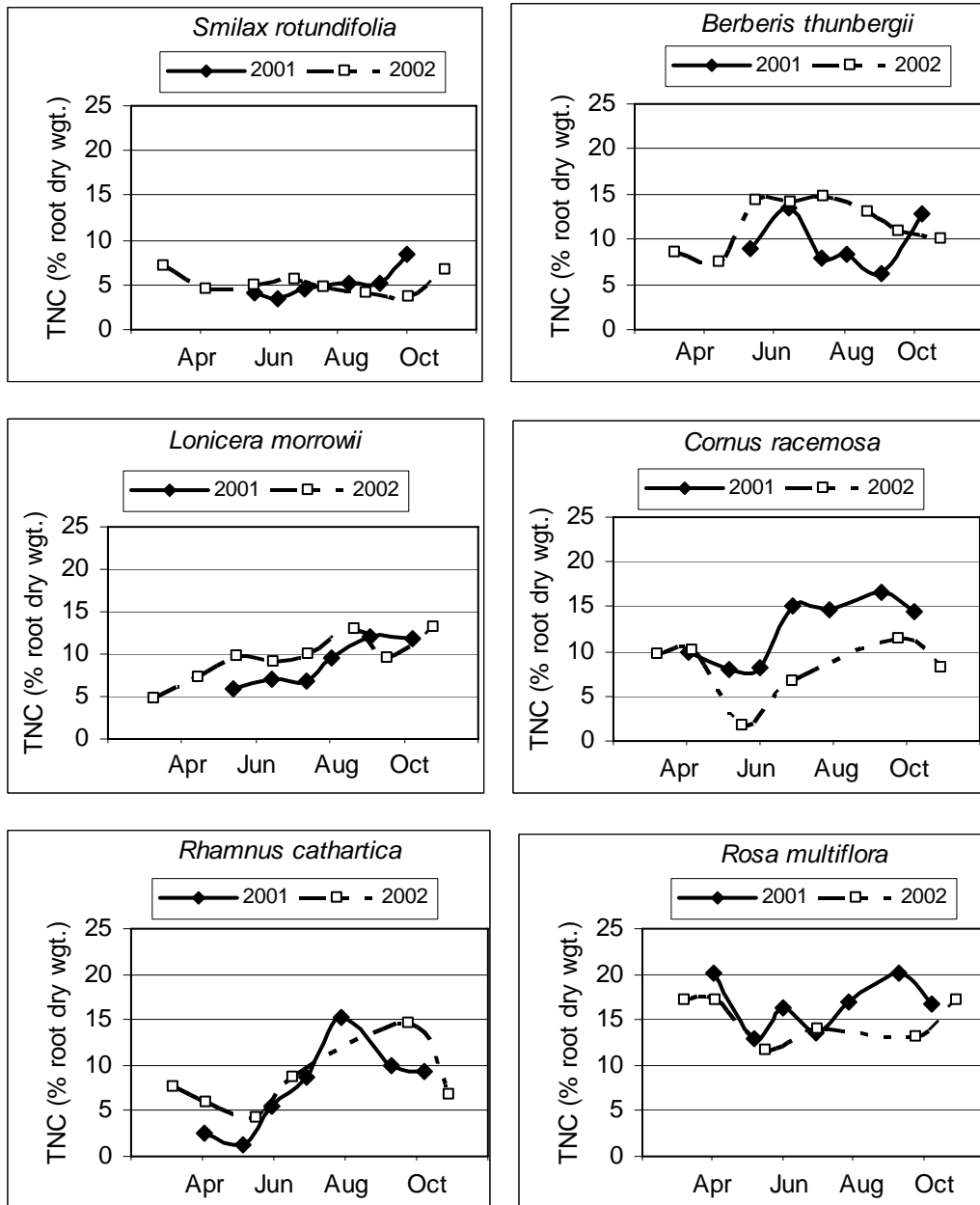
Figure 3-2. Total non-structural carbohydrates (TNC) for *Smilax rotundifolia, Berberis thunbergii, Lonicera morrowii, Cornus racemosa, Rhamnus cathartica,* and *Rosa multiflora* from 2001 -2002.

Table 3-2. Average date of first and last frost and approximate length of growing season for the study sites.

Site	Ave last frost	Ave first frost	Approx. # frost free days
Montezuma, NY	Mid - late April	Mid - late October	185
Sheffield, MA	Mid May	Late September	130
Naushon, MA	Mid April	Mid October	185

Table 3-3. Annual and growing season precipitation (cm) from weather stations close to the study sites (distances are between site and weather station). Normal values are 30-year averages. Shaded cells indicate below-average precipitation.

Site	Annual Precipitation (cm)		
	Normal	2001	2002
Syracuse, NY (50 km)	98.8	86.8	101.5
West Otis, MA (21 km)	118.4	100.6	110.3
Vineyard Haven, MA (15 km)	117.0	107.7	118.6
	Growing season (April – October) Precipitation (cm)		
Syracuse, NY (50 km)	62.9	51.9	70.7
West Otis, MA (21 km)	72.8	60.7	74.5
Vineyard Haven, MA (15 km)	65.5	62.7	55.0

Throughout the region, 2001 was drier than normal with precipitation 10-15% below normal (Table 3-3). Growing-season (Apr-Oct) precipitation was below normal at all of the sites with deficits of 11, 12.1, and 2.8 cm recorded at weather stations near Montezuma, Sheffield, and Naushon respectively. Although no significant correlation exists between the TNC data and the monthly precipitation records for these sites, there are interesting trends. In 2001 TNC levels for *Berberis* were depleted in the spring (prior to my first sampling of roots) and then recovered, but were also unexpectedly depleted

later that growing season (Figure 3-3). The decrease in TNC for *Berberis* occurred when

precipitation was 35-52% below-normal (3.7 & 5.5 cm below normal for July & August

respectively). *Rosa* also experienced a mid-season decline in 2001 that coincided with

below-normal rainfall, whereas the other species were not influenced by precipitation in

2001. In 2002 growing-season precipitation levels returned to or exceeded normal values

at these sites, except for Naushon where precipitation was locally 16% (10.5 cm) lower

than normal during the growing season with July and August precipitation each 7 cm

(87% & 71% respectively) below normal. During this dry period, *Smilax* TNC declined

from 5.7% in July to 3.7% in October 2002.

Discussion

In temperate regions carbohydrate reserves are important for the maintenance,

growth, and survival of woody species. Roots store the most carbohydrates, and the

amount of TNC stored in roots relative to species-specific normal concentrations can be

used as a measure of vigor for a plant (Loescher *et al.* 1990). All six species that I

evaluated followed the general trend of depletion in the spring and replenishment later in

the growing season. Each species generally experienced maximum reserve depletion by

late May following leaf-out (and in some cases flower production), although *Lonicera*

may have reached its maximum depletion earlier. The earliest samples collected for

Lonicera had the lowest of the spring season. In 2002 leaf expansion for *Lonicera* and

Berberis was under way by March 25th and leaves had fully expanded by April 12th.

Spring heat sums may account for year-to-year variation in the timing of spring

TNC minima, as budburst and leaf-out are driven by thermal accumulation for many

species (Lechowicz 1984, Hunter & Lechowicz 1992). *Lonicera* and *Berberis* leafed-out

when the heat sum was low (14; base 4°C). *Berberis*, unlike *Lonicera*, continued to

deplete reserves through March and April before beginning replenishment, so its TNC

minimum was during that period.

At Montezuma *Cornus* and *Rhamnus* leafed-out by mid-April once the heat sum

exceeded 150, but *Rosa* was earlier with leaf-out occurring in late March (heat sum < 40).

Smilax was the last to leaf-out with only 1% of its leaves expanded by late April,

although the heat sum at this time was comparable to those of Montezuma at the time of

Cornus and *Rhamnus* leaf-out. With the exception of *Rhamnus*, the non-native species

leafed-out earlier than native species where they occurred.

Berberis, *Lonicera*, and *Rosa* leafed-out when heat sums were low (< 40), perhaps

indicating a different phenological cue (such as photoperiod) or a threshold appropriate to

their native range (Lechowicz 1984). Batcher and Stiles (2004) suggest that some non-

native species (like *Lonicera* spp.) may gain a competitive advantage by having an

extended growing season (due to early leaf-out and/or a later leaf fall than native

species). These species risk damage from frost, however, as the average last frost is well

after their leaf expansion in the Northeast. In 2001 localized areas on Naushon Island

experienced a late frost. Although the *Smilax* that we sampled did not show any visible

damage due to frost, the late depletion of TNC (in June) may indicate that additional

reserves were needed to support plants following a few days of nighttime freezing temperatures in May and June.

Following initial spring depletion, there was, for the most part, a gradual replenishment of TNC in the roots of all species. Full recovery took most of the growing season - 4 to 5.5 months - except for *Berberis*. Although there were yearly variations in recovery times, *Berberis* had the most rapid and consistent replenishment of reserves, requiring only 31 to 35 days. In 2001 after recovering from a spring deficit in approximately one month (the lowest point in the spring could not be determined), *Berberis* had an unexpected decline resulting in a depletion of reserves equal to or exceeding that of the spring. Reserves remained low throughout the summer and were not replenished until October, with the replenishment again occurring in just one month.

Other factors besides leaf-out can influence the extent of TNC use and replenishment including flowering, disturbances (e.g. defoliation), and water stress (Kramer & Kozlowski 1979, Loescher *et al*. 1990, Wan & Sosebee 1990). In 2002 I noted the timing of leaf-out, flowering, fruiting, and senescence. For *Cornus*, *Rhamnus* and *Rosa*, maximum TNC depletion occurred as flowers were opening. Reserves were replenished even as the fruit was maturing. TNC did not decrease during flowering and fruiting in *Lonicera*, *Berberis*, and *Smilax*. For all six species, flower and fruit production is likely supported by currently produced photosynthate or reserves within above-ground tissues. Declines in TNC following or during senescence occurred for *Cornus* and *Rhamnus* in both 2001 and 2002. The other species' TNC either did not

decline at the end of the growing season, or I only captured a decline in one of the years of the study. These declines in TNC may be due to a shift in reserves from roots to stems to increase cold hardiness and/or to support dormant season respiration (Kozlowski & Pallardy 1997).

Water stress (due to low precipitation, high temperature, and/or soil texture and drainage) can influence the use and storage of carbohydrate reserves. The production of photosynthate is tightly linked to the availability of water (Kozlowski & Pallardy 1997), deficits in which can reduce photosynthesis or shift where photosynthate is used within the plant. Water stress may cause an increase in fine root growth at greater depths (to access available water, Joslin *et al*. 2000), prevent development of reproductive organs, or slow growth entirely. If photosynthesis is slowed, then production of excess carbohydrate is also likely to slow. Precipitation in the southern Berkshires was highly variable during 2001 with some months recording up to 8 cm (50%) above normal, whereas a majority of months were closer to 4 cm (50%) below normal. *Berberis* experienced an unexpected decline in stored TNC from early July through September when monthly precipitation records indicate below-average rainfall (July and August were 35% and 52% below normal, respectively). The plants were able to recover TNC quickly, however, following 8 cm above-normal rainfall in September. Although also sampled in the Berkshires and so subjected to the same pattern of precipitation, *Lonicera* was not as clearly influenced by the lack of rainfall. This may be due to the fact that sample plants were growing in moister soils (in or adjacent to a wetland) than *Berberis*,

which was on a drier, mid-slope site. TNC in both of these species showed no effect of rainfall during 2002, a year with average precipitation throughout the growing season.

Although the Montezuma NWR region also experienced dry conditions in 2001, TNC levels dropped below expected values only in *Rosa*, which generally appears to have a very slow replenishment response. In both years *Rosa* TNC values remained low during the growing season and only replenished during the fall. Naushon Island experienced near normal precipitation during 2001 but was well below normal during the 2002 growing season, with rainfall for the year 13 cm below normal by August. Although *Smilax* began to recover TNC between April and July 2002, dry conditions may have caused the second depletion of TNC between July and October before it was finally replenished in November.

The amount of TNC reserves varies among species and sites, and with time and climatic conditions. The six species that I evaluated followed the general depletion and replenishment cycle described for temperate species (Loescher *et al*. 1990, Kozlowski 1992), although there were differences in the timing of depletion and replenishment between species and years. Spring phenology is influenced by heat sums, which can explain differences in the timing of TNC depletion between years. The four non-native species leafed-out earlier (and depleted their reserves earlier) than the two native species, potentially giving them a competitive advantage. The non-native species leafed-out and depleted TNC while heat sums were low, indicating that heat sums may not be a good predictor of their spring phenology (or that a base other than 4°C should be used).

Precipitation may also influence carbohydrate storage in these species as it influences photosynthesis.

Knowledge of the phenology of TNC and when reserves are likely to be low can guide managers planning treatments to control invasive species. Treatments applied following leaf-out in the spring will result in additional depletion of TNC before it recovers (see Chapter 4). Also, plants stressed by unusual climatic conditions, such as drought, can be further stressed by treatments that deplete their carbohydrate reserves. By applying treatments during anomalous weather patterns (e.g. drought), a manager may achieve greater control of an invasive species than if the treatment was applied during optimal growing conditions.

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CHAPTER 4

RESPONSE OF ROOT CARBOHYDRATE RESERVES TO CUTTING AND

PRESCRIBED FIRE TREATMENTS OF SIX WOODY INVASIVE SPECIES.

<u>Introduction</u>

Woody invasive species are some of the most menacing invaders of native

ecosystems. By both their stature and physiology, these species present formidable

problems for land managers trying to eliminate them from natural areas. Invasive shrubs

such as Japanese barberry (*Berberis thunbergii*), common buckthorn (*Rhamnus

cathartica*), and exotic bush honeysuckles (*Lonicera* spp.) negatively affect natural

communities in the northeastern United States by suppressing understory herbs and tree

seedlings, out-competing native species, and altering ecosystem processes (Woods 1993,

Weatherbee *et al.* 1998, Gould & Gorchov 2000). Permanent elimination of woody

invasive species is difficult due to their ability to sprout from root carbohydrate reserves

following injury or removal of above-ground stems.

Woody species such as trees, shrubs, and vines have generally evolved the ability

to survive natural disturbances (e.g. flooding, fire, wind storms, browsing, and insect and

disease outbreaks) by sprouting. A key component of this survival strategy is to store

enough carbohydrates underground to support growth in the period before photosynthesis

can begin (Kramer & Kozlowski 1960, Loescher *et al.* 1990, Bowen & Pate 1993).

Evaluations of the amount of carbohydrates stored in roots between species that resprout versus those that rely on seed production indicate that sprouters generally store more carbohydrates below ground than do seeders (Bowen & Pate 1993, Bell & Ojeda 1999). Bowen and Pate (1993) report that fire resistant sprouters have disproportionately large roots containing high concentrations of carbohydrates and nutrients compared to species that do not resprout. Sprouters also have lower total-plant growth rates indicating that the storage of resources may be at the expense of growth (Pate *et al.* 1990, Bowen & Pate 1993, Sakai *et al.* 1997, Verdaguer & Ojeda 2002). Invasive species often produce large amounts of seed, but may also spread vigorously through vegetative means with or without disturbance. No studies have evaluated the importance of carbohydrate reserves in invasive shrubs of the Northeast.

For deciduous species, one of the main uses of reserves is to support growth and respiration prior to leaf-out and subsequent production of photosynthate (Cook 1966, Loescher *et al.* 1990, Kozlowski 1992, Rodgers *et al.* 1995, Sakai *et al.* 1997). Depending on the species, one-half to two-thirds of stored reserves can be used to support annual flushing of new leaves and shoots following the dormant season (Kozlowski 1992). These reserves are then replenished during the growing season. Carbohydrate storage contributes to plant vigor: the more reserves, the better an individual will be able to survive stress; whereas depleted reserves often result in plant death (Buwai & Trlica 1977, Gregory & Wargo 1986, Kozlowski 1992). Johansson (1993) reports that low numbers of sprouts or suckers after cutting or defoliation indicate low starch levels in the roots of *Populus tremula*. Due to the annual cycle of depletion and replenishment of

stored carbohydrates, the timing of removal of above-ground biomass influences the sprouting response. Late-season defoliation causes a decrease in carbohydrate reserves which impacts the vigor of the individual at the beginning of the following growing season (Gregory & Wargo 1986, Loescher *et al.* 1990). Cutting or browsing is least detrimental to root reserves and overall plant vigor when done in the winter dormant season (Cook 1966, McConnell & Garrison 1966, Kays & Canham 1991). Kays and Canham (1991) found that for *Acer rubrum*, *Betula populifolia*, *Fraxinus americana*, and *Prunus serotina*, there were species-specific defined periods in the growing season when cutting resulted in low fall starch reserves and low sprout growth rates the next year. These periods were shorter in species with determinate growth patterns, but for both determinate and indeterminate species the optimal cutting time fell between the end of shoot growth in the spring and before the cessation of growth later in the summer (Kays & Canham 1991).

The majority of research on starch reserves in woody species has focused on tree species, particularly broadleaf trees (Wargo 1979, FitzGerald & Hoddinott 1983, Gregory & Wargo 1986, Renaud & Mauffette 1991, Johansson 1993), but the patterns of starch storage and depletion in shrubs appear to be similar to those of trees (McConnell & Garrison 1966, Bowen & Pate 1993, Zasada *et al.* 1994, Droege 1996). Knowing the patterns and timing of starch storage and depletion of invasive woody shrubs compared to non-invasive native vegetation may aid our understanding of why these species are successful invaders (see Chapter 3). Highly invasive species may be better suited to surviving certain stresses due to their ability to grow quickly and perhaps acquire large

reserves to insure against the next stress. This study documents the impacts that

mechanical and prescribed fire treatments (applied at different points in the annual

carbohydrate reserve depletion and replenishment cycle) have on the reserves of six

invasive species in Massachusetts and western New York State.

Methods

Each of six invasive shrub species (*Cornus racemosa*, *Rhamnus cathartica*, *Rosa

multiflora*, *Berberis thunbergii*, *Lonicera morrowii*, and *Smilax rotundifolia*) was studied

at one of three locations. See Chapter 2 for species and site descriptions. At all three

sites (Montezuma NWR, Berkshire Nature Conservancy preserves, and Naushon Island)

managers have used mechanical treatments and/or prescribed fire to control these species

and, in the case of Naushon Island, to reduce fire hazard.

Plot locations and treatments

At each location, four 0.2 ha (40 m x 40 m) plots were located in areas with

similar overstory and understory vegetation in the spring of 2001. The four plots were

randomly assigned to one of four treatments: 1) untreated control, 2) dormant season burn

(or cut if unable to burn), 3) growing season cut followed by a burn in the same season,

or 4) growing season cut. This treatment regimen provided an opportunity to compare

growing season cutting without burning to a cut and burn treatment (treatment 4 vs. 3), as

well as the difference between dormant and growing season treatments. Treatment plots

within any given site were not replicated, but rather were sampled repeatedly over three years. Initial treatments were applied during the summer of 2001 and spring of 2002. All growing season treatments received a second season of cutting during 2002. See Table 4-1 for treatments and dates. In addition, at Montezuma National Wildlife Refuge, a fifth plot was established to compare mowing with a mulching machine (mow) with brushcutting (cut). Treatments were differentially applied at each site based on availability of equipment and personnel, and weather factors.

Root collection and total non-structural carbohydrate analysis

Sections of roots of the study species were collected from each plot approximately once a month during the growing season (except during the several-week period after treatment until above-ground sprouts were identifiable). See Chapter 3 for detailed root collection and total non-structural carbohydrate analysis methods.

Analysis

Each site was evaluated as an independent experiment for the species at the site. Analysis of covariance (ANCOVA) was used to determine if there were significant differences in TNC levels between plots (treatments) with time as the covariate (SYSTAT 10.0). Because the treatments were not replicated, sampling times were used as "replicates" for each treatment. To test the significance of the treatments over time, two ANCOVAs were run: 1) 2001 & 2002 data only, and 2) all data (2001-2003). All

Table 4-1. Treatment protocol with dates.

Plot	2001 treatments	2002 treatments	2003 treatments	Total # treatments
Montezuma NWR – Lay Road – Cornus racemosa, Rhamnus cathartica				
Control	-	-	-	0
Mow/burn	Mow 6/23 Burn 8/24	Mow 6/13 Mow 7/25	-	4
Cut/burn	Cut 7/16 Burn 8/24	Mow 7/25	-	3
Mow-only	Mow 6/23	Mow 7/25	-	2
Dormant	-	Spring cut 4/24	Spring burn 4/25	2
Montezuma NWR – Clark Ridge – Cornus racemosa, Rhamnus cathartica, Rosa multiflora				
Cut-twice	Cut 7/13	Cut 8/14	-	2
Control	-	-	-	0
Dormant	-	Spring cut 4/23	-	1
Cut-once	Cut 7/17	-	-	1
Bartholomew Property – Berkshires – Berberis thunbergii				
Dormant	-	Spring burn 4/19	-	1
Control	-	-	-	0
Cut/burn	Cut 7/6 Burn 11/18	Cut 7/25	-	3
Cut-only	Cut 7/6	Cut 7/25	-	2
Bear Rock Stream Property – Berkshires – Lonicera morrowii				
Control	-	-	-	0
Cut/burn	Cut 7/10 Burn 11/18	Cut 6/13 Cut 7/24	-	4
Dormant	-	Spring cut 4/12	-	1
Cut-only	Cut 7/10	Cut 6/13 Cut 7/24	-	3
Naushon Island – Smilax rotundifolia				
Cut/burn	Cut 6/28 Burn 8/2	Cut 8/6	-	3
Dormant	-	Spring burn 4/5	-	1
Cut-only	Cut 6/29	Cut 8/6	-	2
Control	-	-	-	0

treatments were performed during 2001-2002 (with the exception of a dormant season

burn at Montezuma NWR in April 2003). TNC were sampled on 6-8 sampling dates

during 2001 and 2002 to determine TNC phenology with and without treatments. They

were sampled once at the end of the growing season of 2003 to determine TNC recovery

after one growing season without treatments. Graphical analysis was used to display the

extent of depletion following treatments compared to controls. Because the phenology of

TNC within the roots of plants is cyclical, a wave-form equation ($y = a + b *$

$\sin^2((2\pi*x)/d + c$ where y is TNC at time x, and a, b, c, & d are constants) was fit to the

data from the untreated plot (control) for each species (CurveFit2D, ver. 5.01). To

determine if the TNC contents on the treated plots differed from those of the control,

expected values for the treated plots were calculated using the equations derived from

control data. A t-test of the residuals (observed-expected = 0) was used to determine if

the treated plots differed significantly from the control.

Results

With the exception of *Berberis*, analyses of covariance of TNC indicated

significant differences between plots (treatments) for each species at each site during the

period from 2001-2002. After one year without treatments (2003), only three species

remained significantly impacted by the treatments (*Rhamnus*, *Lonicera*, *Smilax*;

ANCOVA with 2001-2003 data, Table 4-2). The TNC sampled in October 2003 showed

that for all plots and species, TNC had recovered approximately to control levels by that

date (Figure 4-1).

Table 4-2. ANCOVA p-values for treatment and time effects for two multiple-year models. (Bold indicates a significant value, p < 0.05. * = interaction term is significant, p < 0.05).

	Treatment		Time	
Species/site	2001-2002	2001-2003	2001-2002	2001-2003
Cornus racemosa / Lay Road	**0.045**	0.143	**0.000**	**0.016**
Rhamnus cathartica / Lay Road	**0.028**	**0.027**	0.059	**0.025**
Rosa multiflora / Clark Ridge	**0.029**	0.153	**0.017**	0.259
Berberis thunbergii / Bartholomew	0.315*	0.332	**0.026***	**0.025**
Lonicera morrowii / Bear Rock Stream	**0.000***	**0.000**	**0.038***	0.909
Smilax rotundifolia / Naushon	**0.002***	**0.008***	0.574*	**0.001***
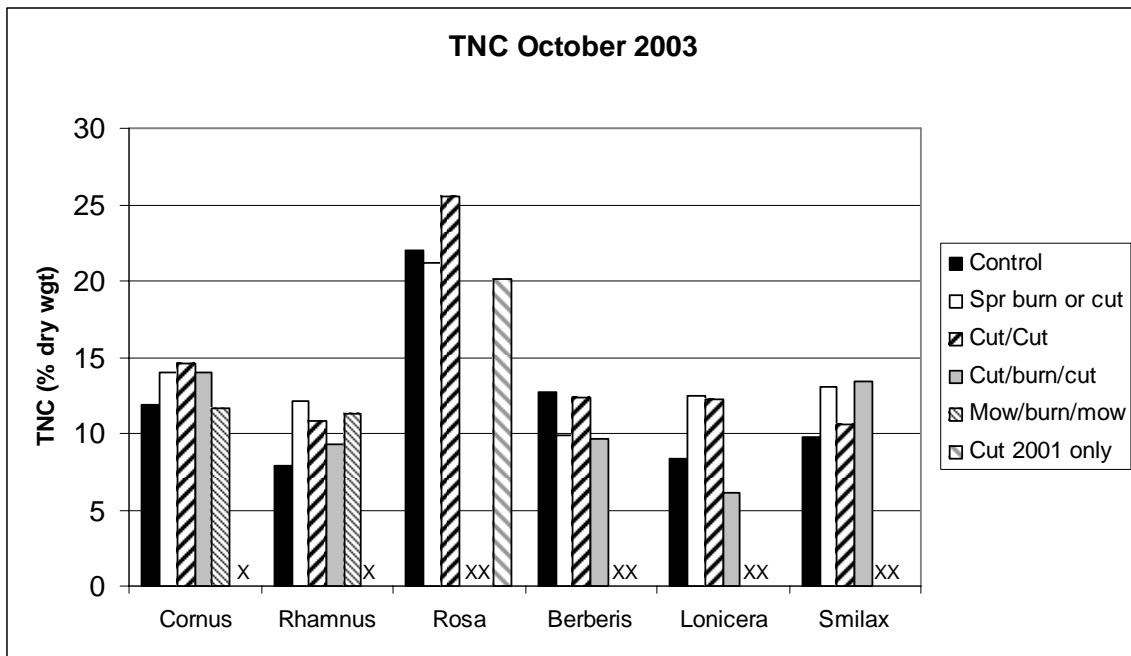
Figure 4-1. Total non-structural carbohydrates (TNC) sampled in October 2003 for all species and treatments. Treatments are listed in Table 4-1. All except the spring (spr) treatments were applied during the growing season. Treatments not applied for each species indicated by "x".

Cornus racemosa

Treatments applied during the study included a combination of mowing, brushcutting, and burning (see Table 4-1). In 2001 two different growing-season-cut treatments were applied: mow on June 23rd (for both the mow-only and the mow/burn plots) and brushcut on July 16th (for the cut/burn plot). *Cornus* TNC stores had begun to recover from their spring lows in the brushcut and the mow-only plants prior to the first treatment, but not in the mow/burn plants (Figure 4-2). Yet all of these treatments caused a reduction in TNC compared to the control plants. A second treatment (prescribed burn on August 24th) in that growing season resulted in *Cornus* TNC in the two burn plots (mow/burn & cut/burn) not recovering to control levels by the end of the first growing season. The mow-only plants (mowed just once on June 23rd) did recover to control TNC levels by October 2001.

During the second year (2002), a new plot was treated with a dormant season (April 24th) cut, and the 2001 growing-season-treated plots received either one or two mowing treatments (mow/burn mowed on June 13th and July 25th, cut/burn and mow-only mowed on July 25th). The dormant-season-cut plants depleted their reserves earlier than those on the control plot, but recovered to control levels by the end of the summer. TNC of the mow-only plants followed the control curve trajectory, even after the second-year mow. The mow/burn and cut/burn plants remained lower than those of the control until November when the mow/burn plants recovered to the control level. Although the cut/burn plants remained lower, their reserves were at least partially replenished after

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Figure 4-2. Total non-structural carbohydrates (TNC) for *Cornus racemosa* from 2001-2003. Stars along the x-axis indicate timing of treatments listed in Table 4-1. All except the dormant cut/burn treatment were applied during the growing season.

being mowed in 2002. When tested with ANCOVA, treatment effects were significant

for 2001-2002 (p=0.045). In the spring of 2003, the dormant season plot (previously cut

in spring 2002) was burned. *Cornus* TNC values in this plot were close to control levels

in the fall prior to the spring burn and were again similar in October 2003. An ANCOVA

completed using the entire data set (2001-2003) indicated a non-significant treatment

effect (p=0.143), but a significant effect of time (the covariate) (Table 4-2).

The wave-form equation derived from the *Cornus* control data captured much of
the variation in the data (r^2=0.65, p=0.012) and was therefore a suitable equation to test
the relationship between the control and treatment plants (Figure 4-3). Observed TNC
values were generally lower than expected for the two summer treatments that included
burning (mow/burn and cut/burn) (Figure 4-3). T-tests of these residuals (mow/burn and

Figure 4-3. Plot of observed versus predicted total non-structural carbohydrates (TNC)
for *Cornus racemosa*. Predicted values are from the equation derived from the control
data.

cut/burn) were significant (p=0.056 and 0.025 respectively), indicating that TNC following these treatments departed from that expected from the derived equation for *Cornus*. Residuals for the growing-season mow-only and the dormant-season-treated plants were not significantly different from zero (p=0.665 and 0.665 respectively).

Rhamnus cathartica

Treatments for this species were the same as described for *Cornus*, as both were sampled from the same plots (see Table 4-1). In 2001 all summer treatments resulted in reduced TNC (Figure 4-4). In 2002 the dormant-cut treatment (cut on April 24) had little impact on TNC, whereas the treatments that were applied during the growing season prevented TNC replenishment until the end of the growing season. Treatment effects on TNC were significant (ANCOVA for 2001-2002, p=0.028). No treatments were applied to any plot after the spring of 2003, and the ANCOVA for 2001-2003 was also significant (p=0.027), although TNC levels on all plots exceeded the control in October 2003.

The wave-form equation derived for *Rhamnus* significantly fit the control data (r^2=0.58, p=0.030). Comparisons of dormant-treatment observed TNC to those predicted by the derived equation indicate a nearly perfect fit (t-test p=0.981, Figure 4-5). The only treatment that resulted in a significant departure from the derived equation was the cut/burn treatment (t-test p=0.010) where TNC were generally lower than predicted (Figure 4-5).

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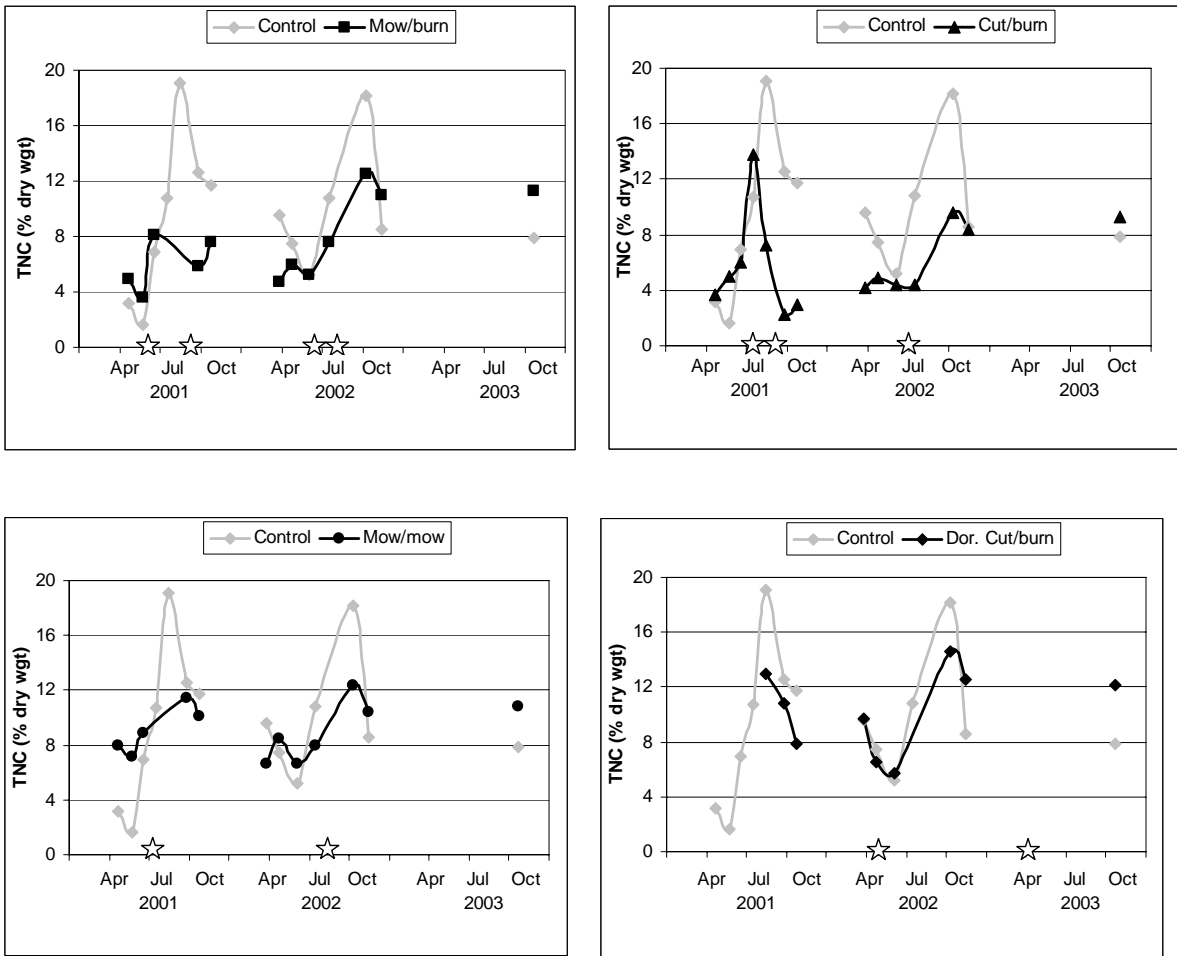
Figure 4-4. Total non-structural carbohydrates (TNC) for *Rhamnus cathartica* from 2001-2003. Stars along the x-axis indicate timing of treatments listed in Table 4-1. All except the dormant cut/burn treatment were applied during the growing season.
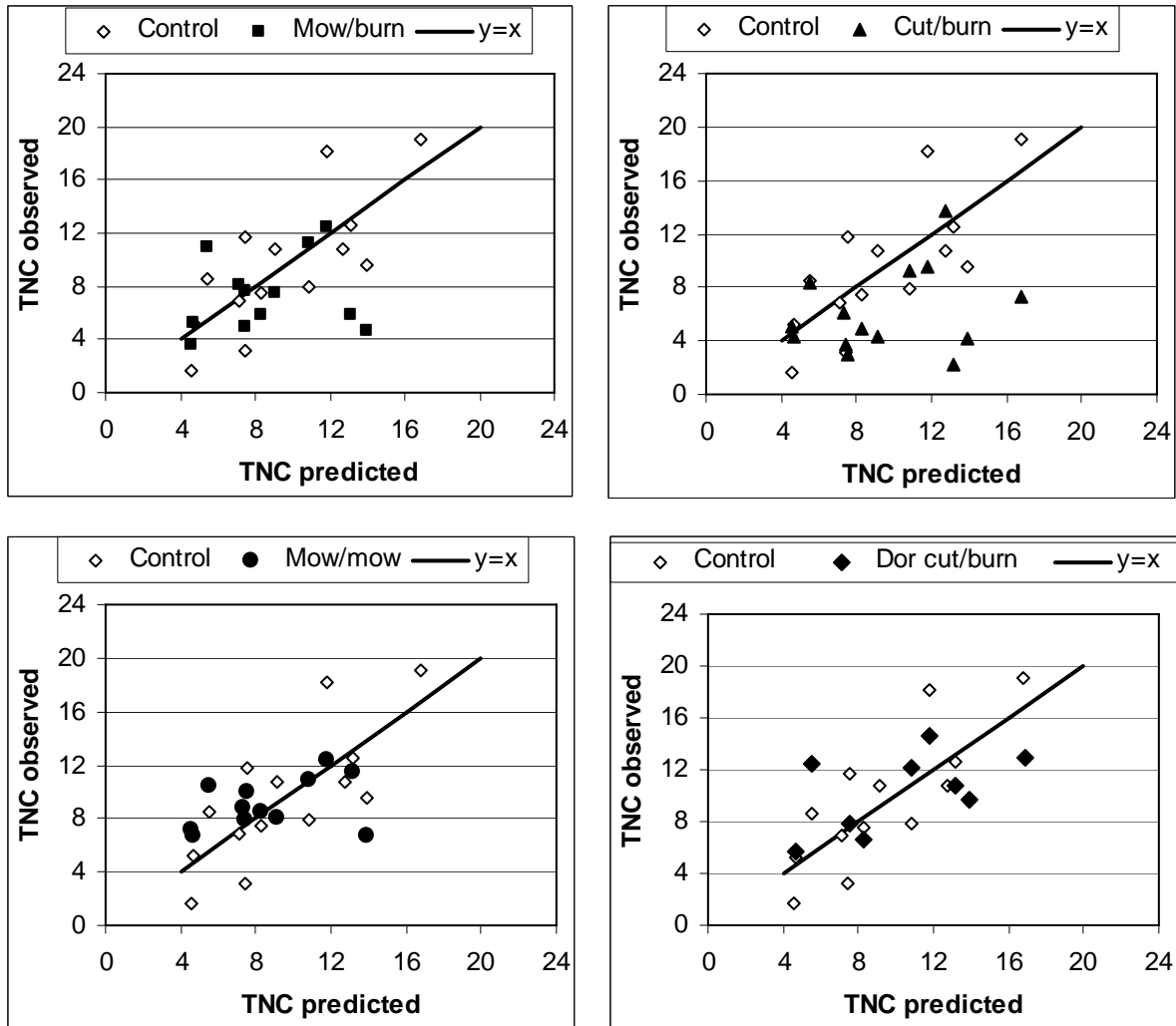
Figure 4-5. Plot of observed versus predicted total non-structural carbohydrates (TNC) for *Rhamnus cathartica*. Predicted values are from the equation derived from the control data.

Rosa multiflora

Cut treatments were applied to two plots in mid-July 2001, and only temporarily reduced TNC levels. The dormant-season cut was applied in the spring of 2002 (April 23rd) and TNC were also only temporarily reduced. The cut-twice plot received its second cut in the summer of 2002 (August 13th). Plants within both plots cut during the

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2001 growing season (cut-twice and cut-once) had TNC levels well below the control

until the end of the 2002 growing season when the cut-once plants recovered to those of

the control plants. The ANCOVA for 2001-2002 was significant (p=0.029). By October

2003 however, even the cut-twice plants recovered to above the control TNC level.

Overall, TNC were not significantly affected by the treatments across the three years of

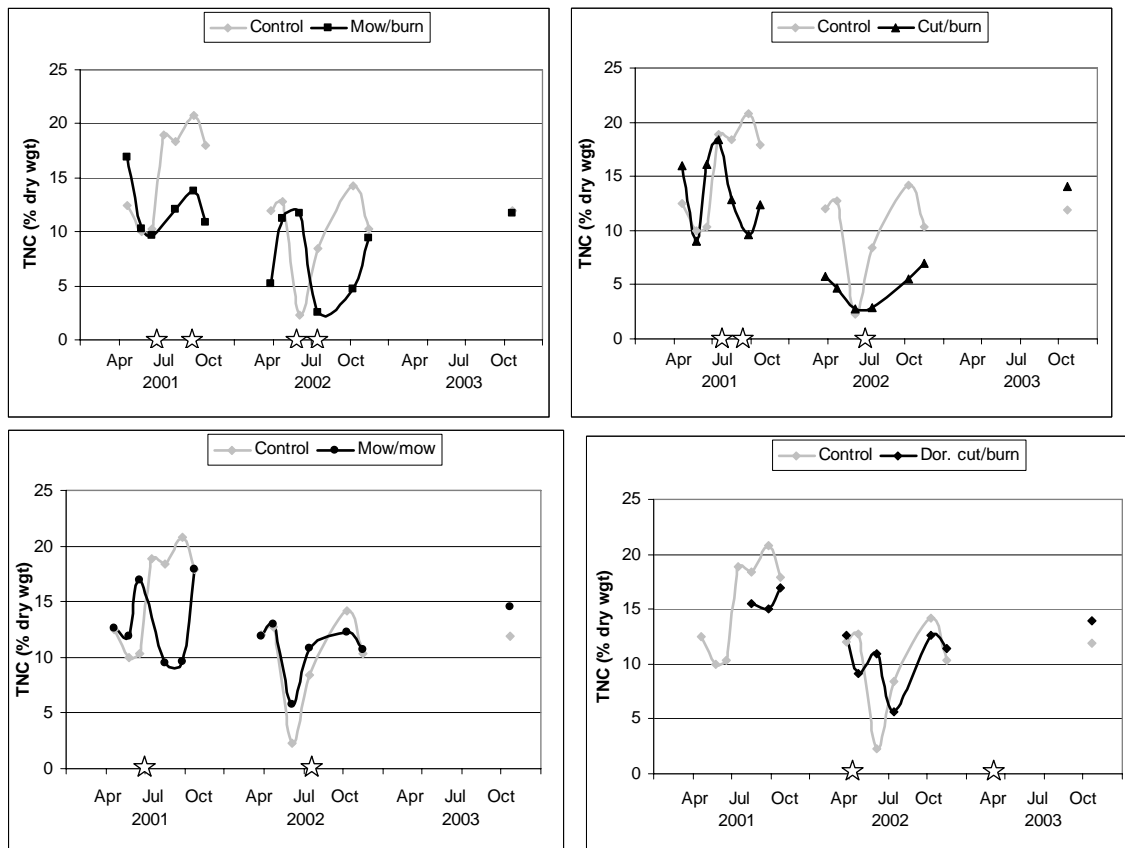the study (ANCOVA for 2001-2003 p=0.153).
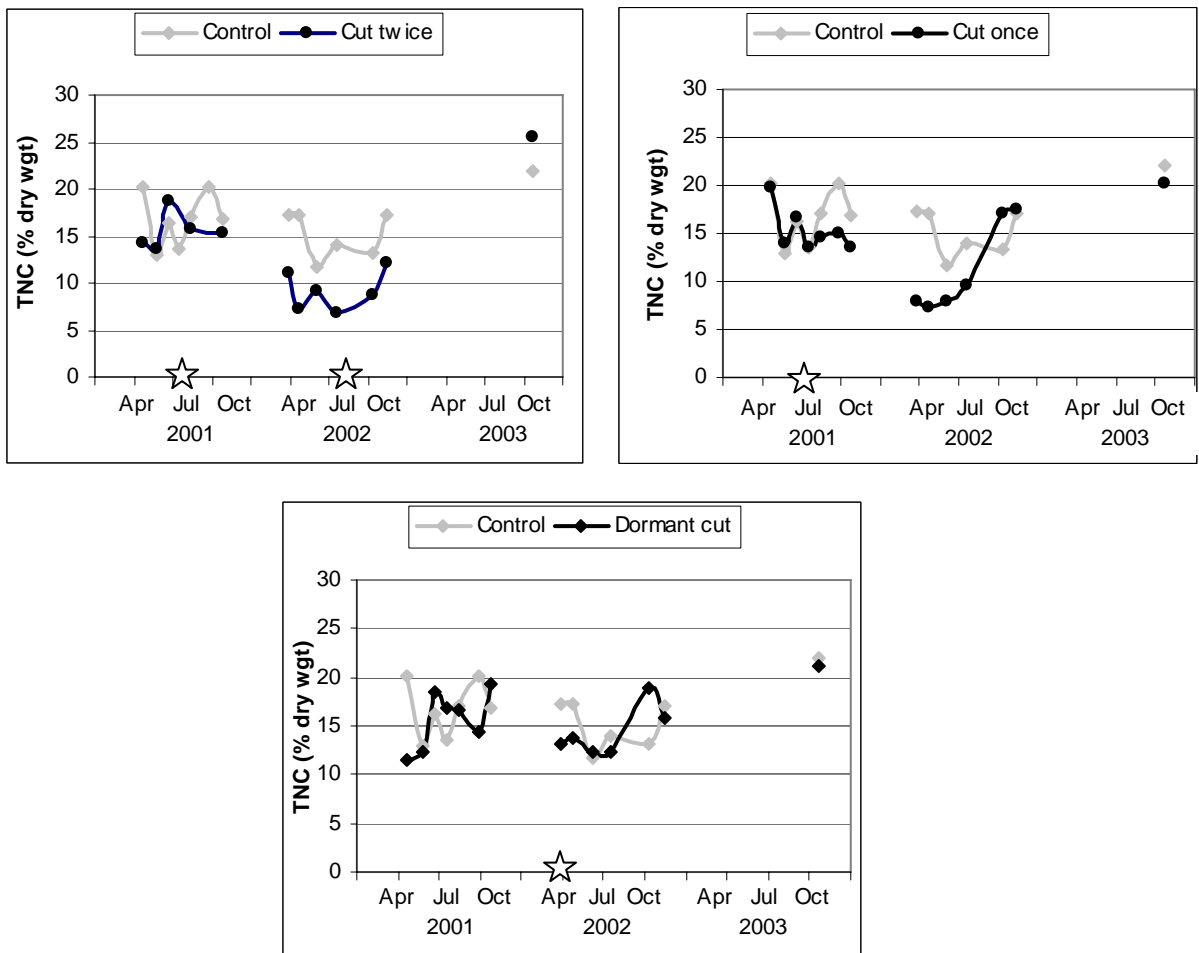
Figure 4-6. Total non-structural carbohydrates (TNC) for *Rosa multiflora* from 2001-
2003. Stars along the x-axis indicate timing of treatments listed in Table 4-1. All except
the dormant cut treatment were applied during the growing season.

The wave-form equation derived for *Rosa* did not significantly fit the control data (r^2=0.30, p=0.292). The residuals from all treatments were also non-significant, although values for the cut-twice plot were generally lower than predicted (Figure 4-7).
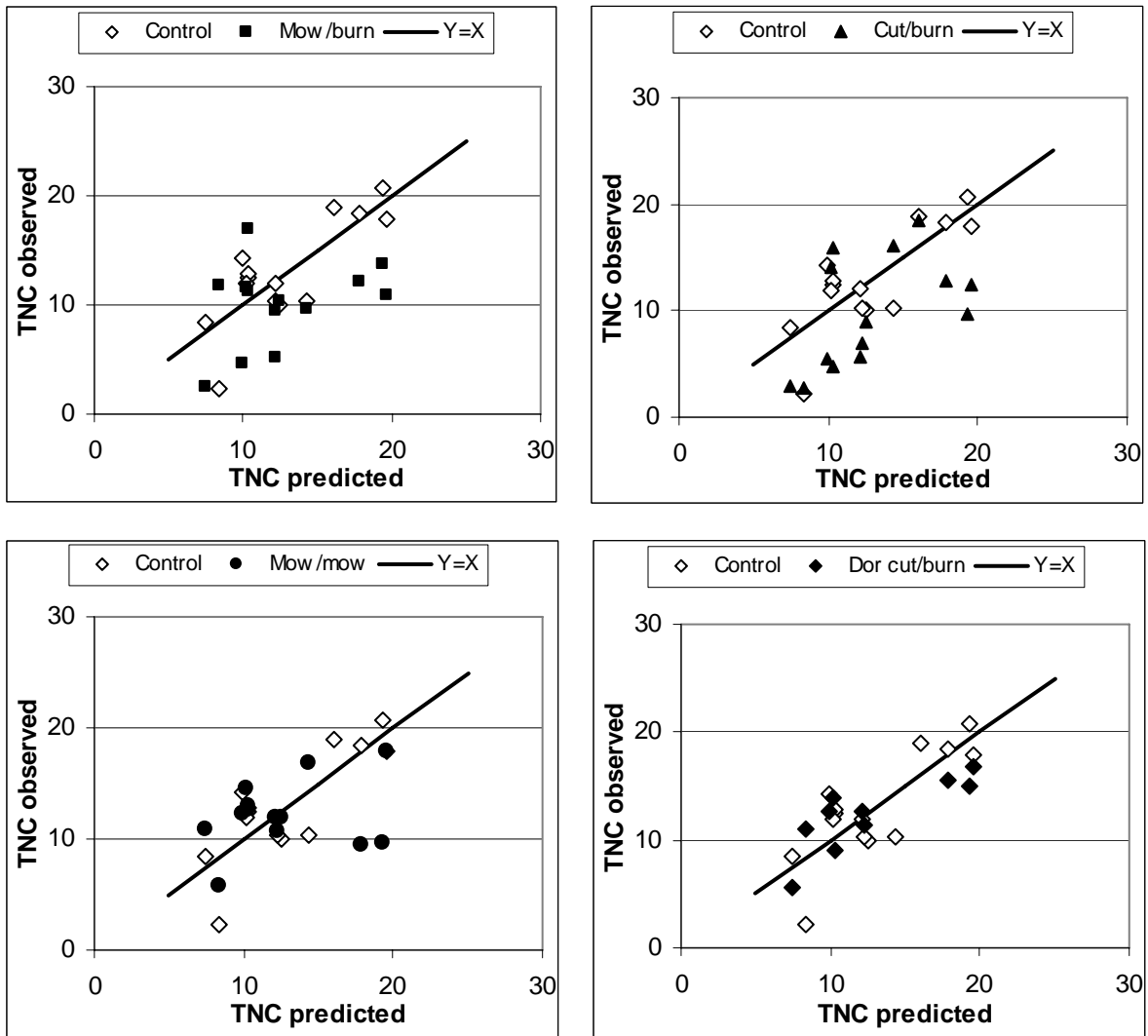

Figure 4-7. Plot of observed versus predicted total non-structural carbohydrates (TNC) for *Rosa multiflora*. Predicted values are from the equation derived from the control data.

In 2001 TNC levels for *Berberis* (control) were depleted in the spring (prior to the first sampling of roots), and then recovered, but were also unexpectedly depleted later in the growing season (Figure 4-8). This second depletion of reserves may have coincided with the depletion of reserves due to cutting treatments, but I do not know if the depletion in the treated plots was due to treatments or the factor (perhaps drought - see Chapter 3) affecting the control plot. All TNC levels were very similar throughout 2001, with TNC levels in the growing-season-cut plants temporarily higher than those of the control during the unexplained depression in the later. A burn was attempted during August 2001, but fuels were too sparse to carry the fire. A second burn after leaf-fall in November 2001 was successful. In 2002 there was the expected single depletion of TNC in the control plants, and all treated plants remained depleted throughout the growing season. A "dormant" season prescribed fire was accomplished in early April, at which time the *Berberis* had already leafed-out, whereas native species had not. Although TNC were reduced in 2002, the ANCOVA of the 2001-2002 data was not significant (p=0.315), perhaps due to the anomaly in the 2001 data set. After one growing season without treatments, TNC in the treated plants returned to levels comparable to those of the control (ANCOVA of 2001-2003 data, p=0.332).
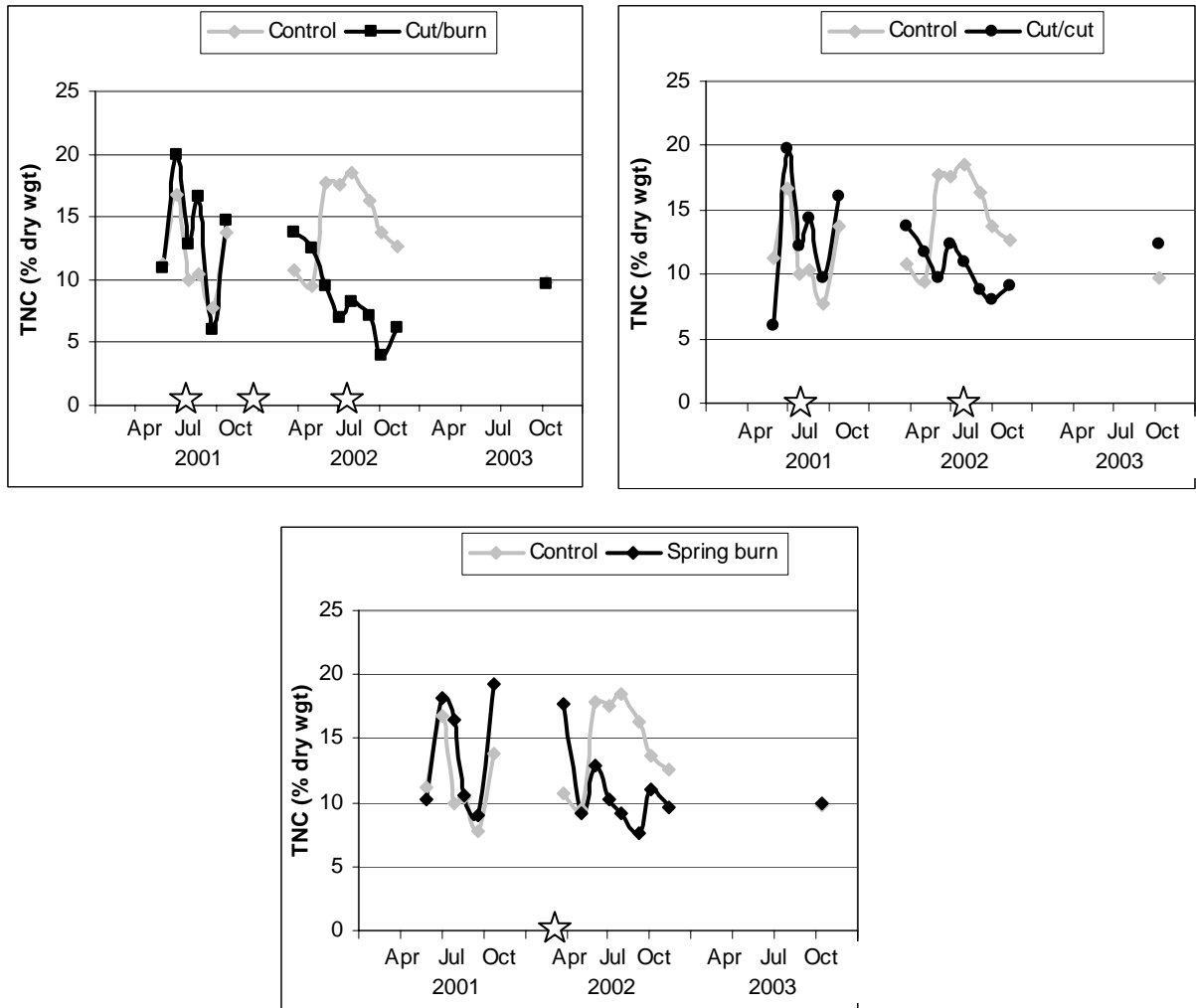
Figure 4-8. Total non-structural carbohydrates (TNC) for *Berberis thunbergii* from 2001-2003. Stars along the x-axis indicate timing of treatments listed in Table 4-1. Note: the dormant burn treatment was after growth had begun in *Berberis*.

Although the derived wave-form equation for *Berberis* appears to explain much of the variation in the data, it is not significant (r^2=0.40, p=0.122). Comparisons of the treatment residuals were also not significant, although the growing-season treatments were generally lower than predicted (Figure 4-9).
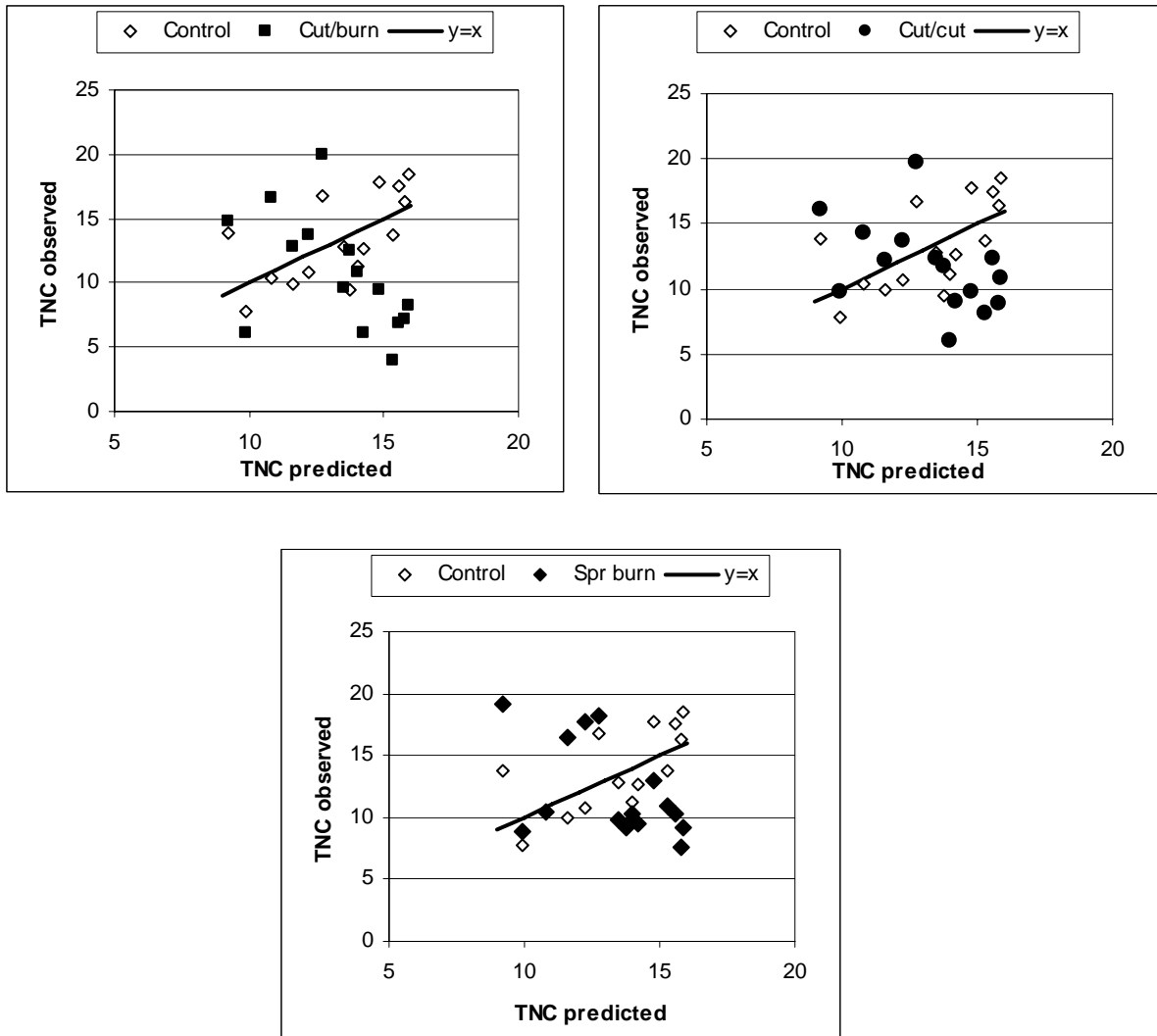
Figure 4-9. Plot of observed versus predicted total non-structural carbohydrates (TNC) for *Berberis thunbergii*. Predicted values are from the equation derived from the control data.

Lonicera morrowii

Treatments applied in 2001 included cutting of plots in early July and an unsuccessful attempt to burn one of the cut plots in August. Cutting treatments did result in significant TNC depletions, with all treatment values lower than in the control (Figure 4-10). As with the *Berberis* plots, the burn treatment was successfully applied following

leaf-fall in 2001. A dormant-season-cut treatment was applied in April 2002, and

additional growing-season-cut treatments in 2002 produced additional significant

depletions in TNC (ANCOVA for 2001-2002, p=0.000). Unlike species previously

discussed, TNC for treated *Lonicera* remained significantly different through October

2003 (ANCOVA for 2001-2003, p=0.000), although some of this difference is likely due
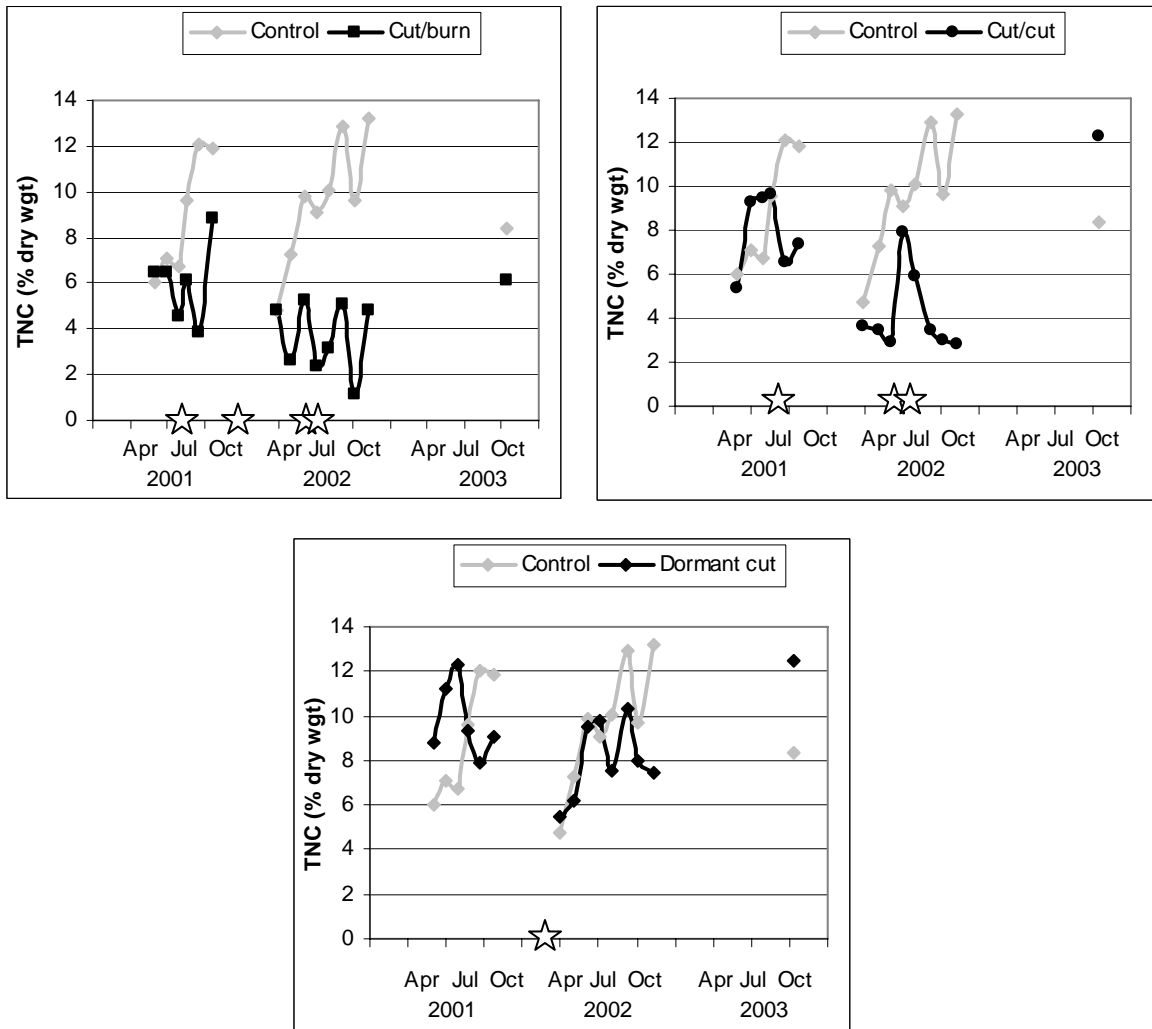
Figure 4-10. Total non-structural carbohydrates (TNC) for *Lonicera morrowii* from 2001-2003. Stars along the x-axis indicate timing of treatments listed in Table 4-1. All except the dormant cut treatment were applied during the growing season.

to the lower-than-expected TNC in the control plants. The cut/burn plot was treated a total of four times during the study – once during the 2001 growing season, once during the fall of 2001, and twice during the 2002 growing season - and remained depleted through the end of 2003.

The wave-form equation derived for *Lonicera* significantly fit the control data (r^2=0.72, p=0.002). Comparisons of the residuals from the two summer treatments (cut-only and cut/burn) were significant (t-test, p=0.008 and 0.000 respectively), indicating that the TNC of these treatments were lower than those predicted (Figure 4-11). Residuals of the dormant-season-cut plot were not significantly different (p=0.770).

Smilax rotundifolia

Smilax had significantly lower TNC levels in control plants than the other six species I studied. Graphs of the 2001 samples indicate large differences among treatments. TNC in plants with treatments applied during the growing season (cut-only and cut/burn) were depleted relative to those of the control, whereas the dormant-treatment plants' TNC remained at or above control levels recorded prior to their treatment. The dormant-season treatment (burn) was applied in the spring of 2002, and the growing-season-treated plants were cut again later that year. TNC in the dormant-burned plants were depleted relative to the control for a few months before recovering to the control level by the end of 2002. The growing-season-cut/burn plants also replenished TNC during 2002,
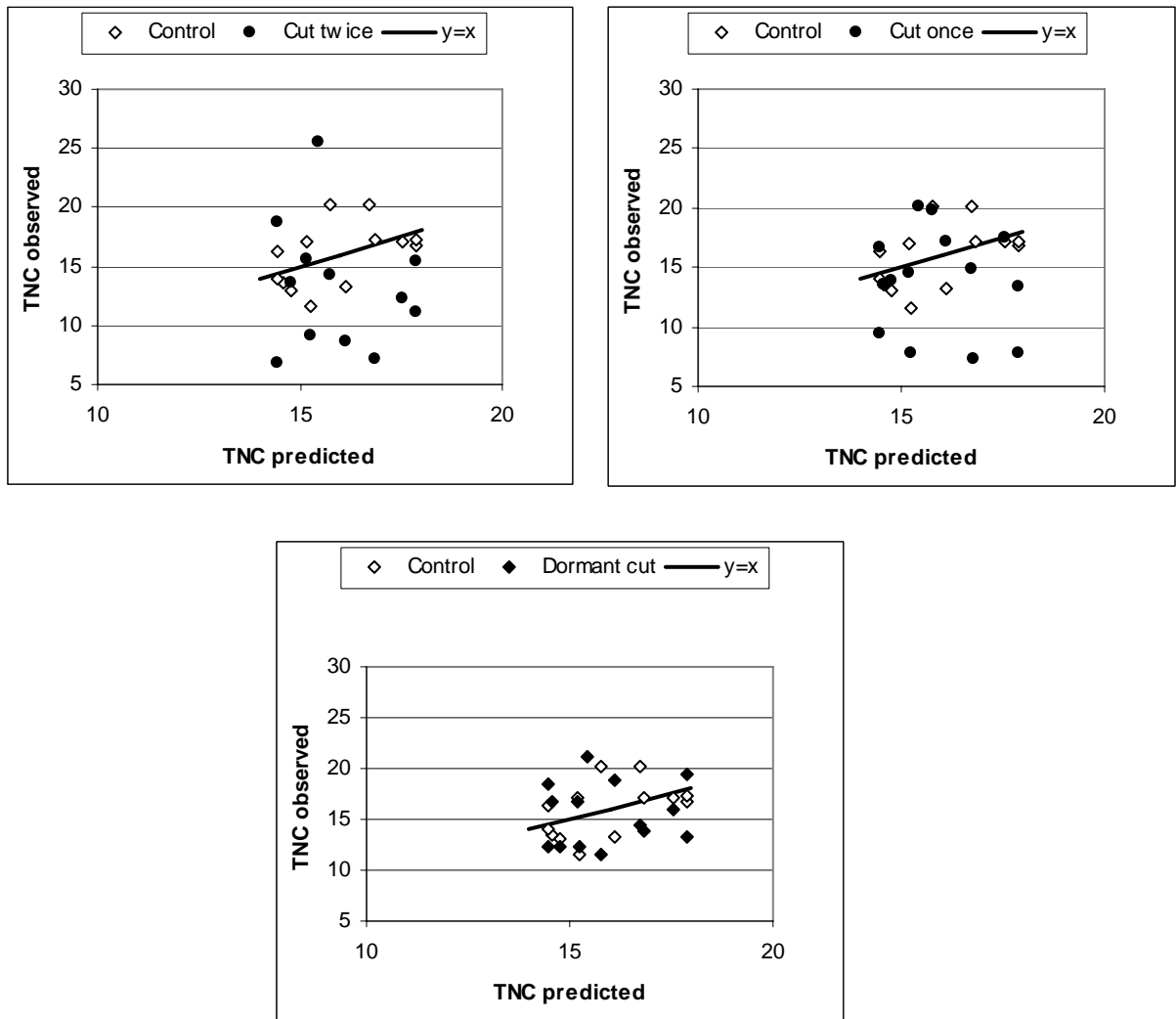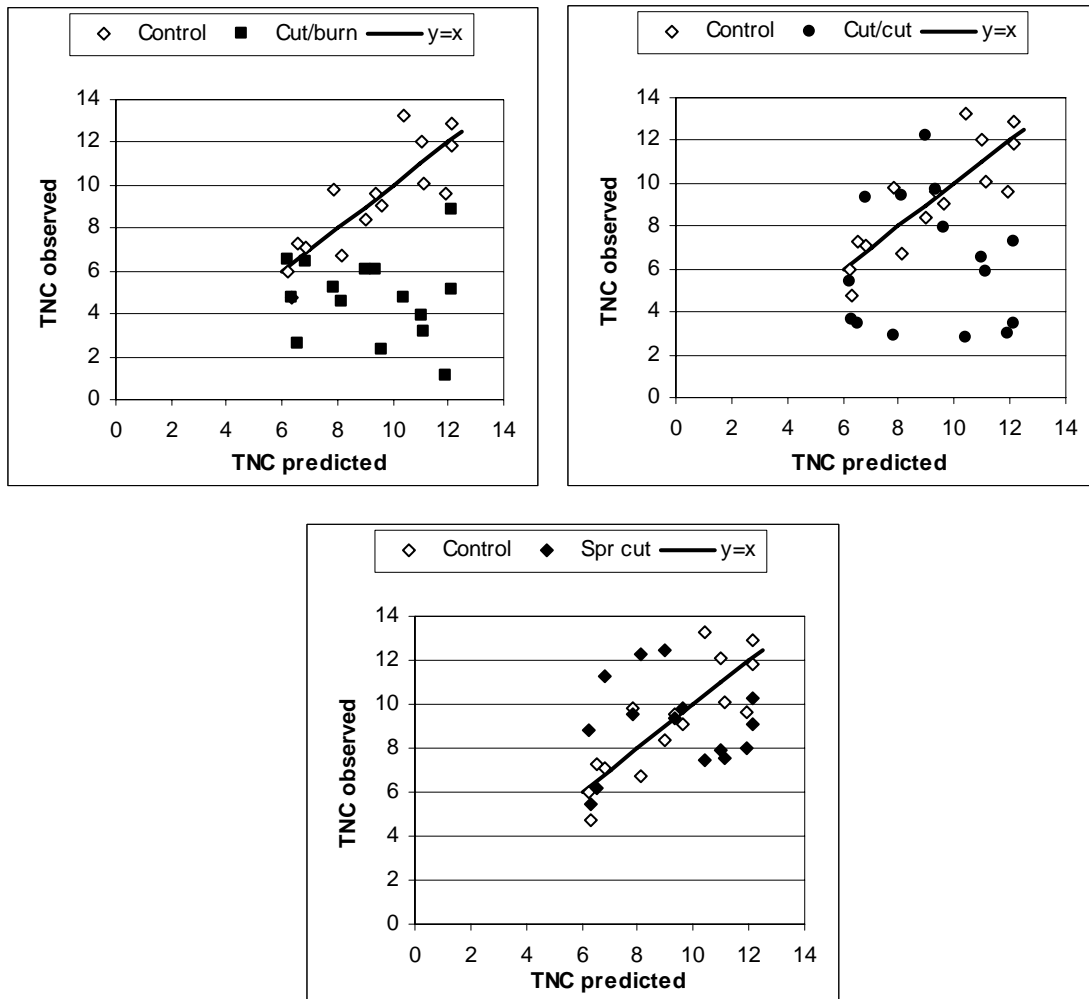
Figure 4-11. Plot of observed versus predicted total non-structural carbohydrates (TNC) for *Lonicera morrowii*. Predicted values are from the equation derived from the control data.

even after being cut a second time on August 6th. Only the cut-only plants (cut once in 2001 and once in 2002) had lower TNC than the control at the end of 2002. The ANCOVA for 2001-2002 was significant (p=0.002). As with *Lonicera*, differences in TNC of *Smilax* remained significant following one growing season without treatments (2001-2003 ANCOVA p=0.008), but all of the treated plants had TNC levels higher than the control in October 2003.
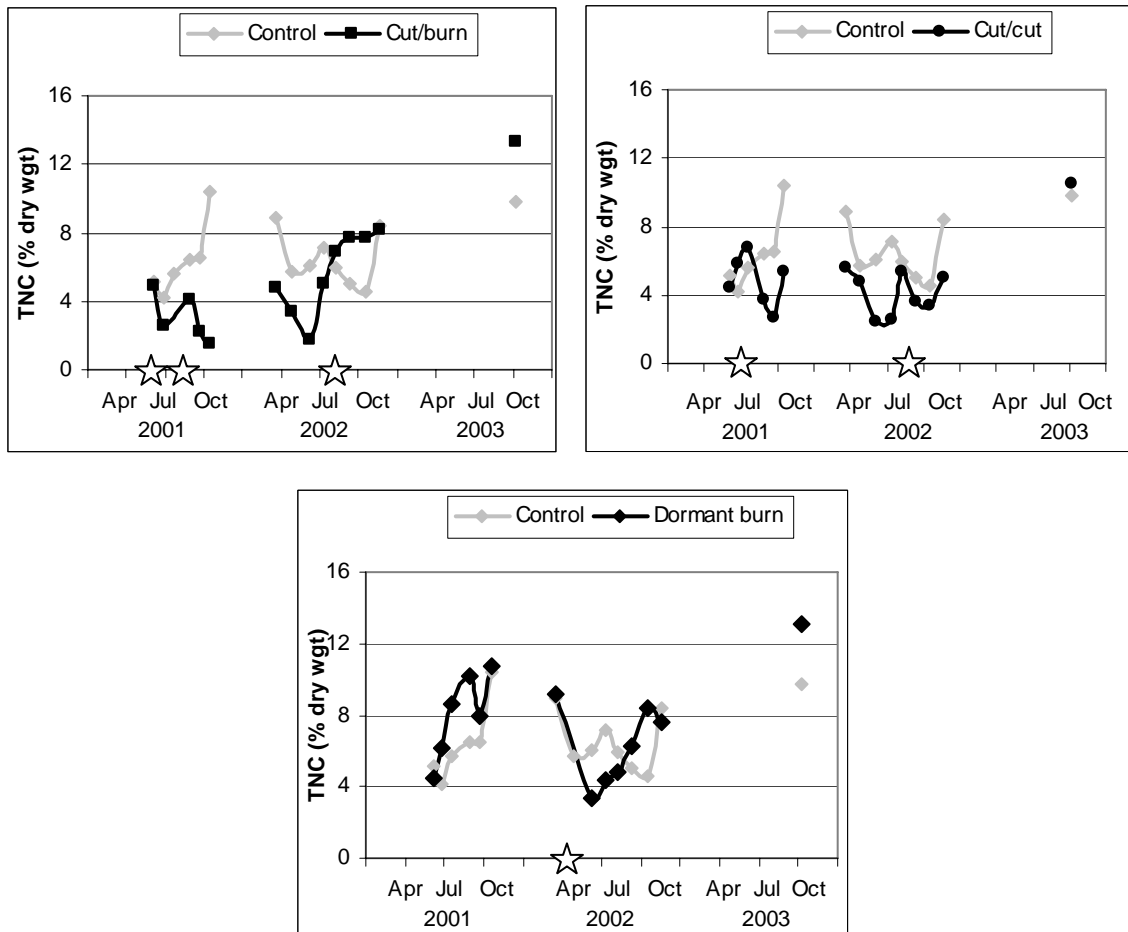
Figure 4-12. Total non-structural carbohydrates (TNC) for *Smilax rotundifolia* from 2001-2003. Stars along the x-axis indicate timing of treatments listed in Table 4-1. All except the dormant burn treatment were applied during the growing season.

The derived wave-form equation for *Smilax* did not significantly explain the control data (r^2=0.34, p=0.197). The observed-minus-predicted TNC values from the summer-cut-only treatment significantly varied from zero (p=0.009), with observed levels generally lower than predicted (Figure 4-13).
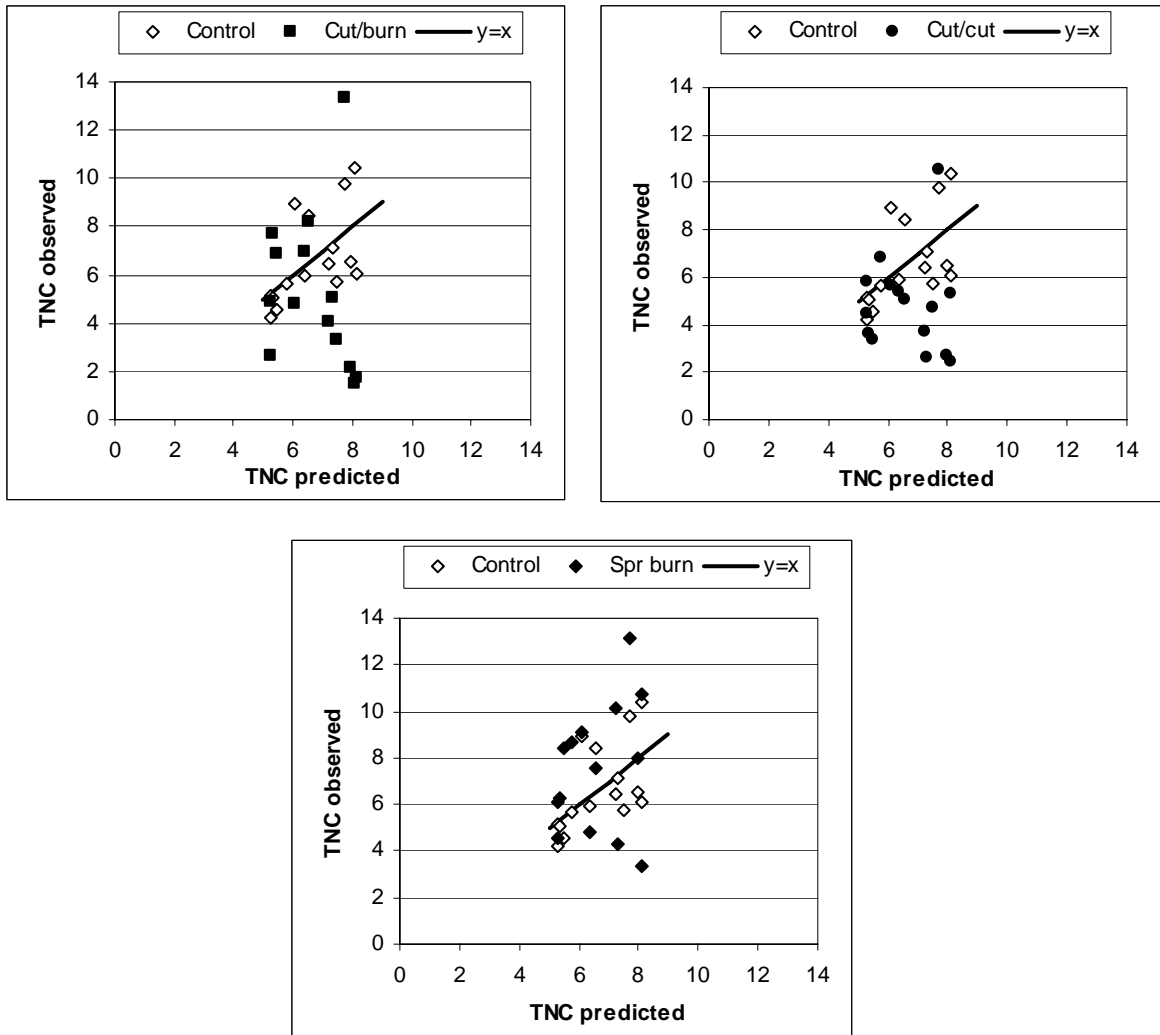
Figure 4-13. Plot of observed versus predicted total non-structural carbohydrates (TNC) for *Smilax rotundifolia*. Predicted values are from the equation derived from the control data.

Discussion

Invasive woody species alter the composition, structure, and fuels of natural

habitats (Gordon 1998, Mack & D'Antonio 1998, Myers & Bazely 2003, Brooks *et al.*

2004). Efforts to control or eliminate these species often focus on removal of above-

ground stems with the hopes of having a lasting impact on the whole plant. This often leads to failed control attempts as treated plants sprout from buds located on rhizomes, roots, or residual stems. Carbohydrate reserves stored in these structures support the growth of sprouts with greater reserves resulting in more vigorous and successful sprouting. I hypothesized that by timing treatments to periods when the invasive species is most vulnerable (i.e. when TNC reserves are low), control efforts are more likely to be successful.

Dormant treatments (whether cutting or prescribed fire) applied during the course of this study resulted in sprouting and quick replenishment of below-ground carbohydrate reserves; often complete replenishment within only a few months and in most cases by the end of the growing season following the treatment. Although dormant treatments changed the structure of the target species by reducing their above-ground abundance within the plots by as much as 75% (see Chapter 5), the plants' TNC reserves allowed vigorous sprouting in all six species I studied. The rapid growth rate of many of these species is likely to lead to the vegetation becoming similar to pre-treatment stature and composition within just a few years as suggested by Dunwiddie *et al.* (1997). Dormant-season treatments do not eliminate invasive species or even decrease their abundance for anything more than one growing season.

The only "dormant" season treatment resulting in lower TNC levels in the fall of 2002 was a prescribed burn of *Berberis* in April 2002. Although applied in early April

before leaf-out of native species, *Berberis* leaves had flushed, so this treatment should be considered a growing-season treatment.

Growing-season treatments generally took longer to recover reserves than dormant-season treatments. Initial growing-season treatments were applied when reserves were thought to be at their lowest, although in practice initial treatments were done at various stages of TNC replenishment following spring lows (due to logistical problems and not evaluating the target species' TNC reserve cycles for at least one cycle prior to treatments). After a single growing-season treatment, reserve levels remained depleted for the rest of the growing season for *Cornus*, *Lonicera*, *Smilax*, and the April-treated *Berberis*. *Rhamnus*, *Rosa*, and the July-treated *Berberis* recovered. Multiple treatments during a single growing season kept TNC reserves low during the season of treatment and into the next growing season. The reserves were further depleted when treated again the following summer. Following these treatments, TNC levels were reduced from between10% to nearly 90% through the remainder of the season, although some recovery was apparent in all species.

For the six species I studied, two years of treatments did not deplete TNC reserves enough to kill plants, although sprouting in TNC-depleted individuals was less vigorous than those with more TNC (e.g. dormant-season treated individuals, see Chapter 5). Mowing or cutting just once in early summer in two consecutive years reduced TNC in *Cornus*, *Rhamnus*, *Rosa*, *Berberis*, and *Smilax*, but plants recovered after one growing season without additional treatment (Table 4-3). *Lonicera* was treated with two cut

Table 4-3. Percentage decrease/increase of TNC in treated plants compared to controls in October 2001, 2002, & 2003. Treatment type and year of treatment are both indicated. All treatments were applied in the growing season except where indicated.

	2001	2002	2003	2001	2002	2003	2001	2002	2003	2001	2002	2003
	Mow Burn	Mow Mow		Cut Burn	Mow		Mow	Mow			Spring Cut	Spring Burn
Cornus racemosa	-39%	-67%	-2%	-31%	-61%	+17%	0%	-14%	+22%	-6%	-11%	+17%
Rhamnus cathartica	-35%	-31%	+42%	-75	-47%	+17%	-14%	-32%	+37%	-33%	-20%	+53%
				Cut01			Cut	Cut			Dor. cut	
Rosa multiflora				-20%	+29%	-9%	-8%	-35%	+16%	+15%	+43%	-4%
				Cut Burn	Cut		Cut	Cut			Spring burn	
Berberis thunbergii				+7%	-71%	-2%	+16%	-41%	+26%	+39%	-20%	+1%
				Cut Dor.burn	Cut Cut		Cut	Cut Cut			Dor. cut	
Lonicera morrowii				-25%	-88%	-27%	-38%	-69%	+46%	-23%	-17%	+49%
				Cut Burn	Cut		Cut	Cut			Dor. burn	
Smilax rotundifolia				-86%	+67%	+37%	-49%	-26%	+8%	+3%	+84%	+34%

treatments during the second growing season due to its prolific sprout growth, and this regimen reduced TNC by nearly 70% at the end of the second growing season. Plants that were treated with a cut-and-burn treatment in the first growing season followed by a single cut in the second growing season had the lowest TNC levels measured at the end of 2002, except for *Smilax* plants. The *Smilax* that was cut once in each treatment year had the lowest TNC of all *Smilax* treatments, although heavy grazing of sprouts by deer could have influenced results for this plot.

All treatments in this study impacted TNC levels for a period of time, but no treatment effect was apparent by October 2003 with the exception of *Lonicera* treated four times over two years (cut01, dormant burn01, cut02, cut02). In fact, in most instances TNC of treated plants were higher in October 2003 than in the untreated controls (Table 4-3). This may be due to an overall reduction in biomass, both above- and below-ground, that decreases the amount of carbohydrates required for respiration, a reduction in the size and density of competitors, or an increase in available nutrients (Belsky *et al.* 1993). Approximately half of photosynthates produced during any time period are used in respiration (Lambers *et al.* 1998). Carbohydrates produced in leaves are used in respiration and growth of leaves and other tissues, before excess is accumulated as reserves (Kozlowski 1971). Therefore, the amount of carbohydrates that can be stored depends not only on the amount of foliage available to produce photosynthate, but also on the total living (respiring) biomass of the plant. Put more simply, larger plants need to produce more photosynthate to grow and maintain their tissues than smaller plants. When a plant has sprouted following removal of above-

ground structures, the young vigorous sprouts maximize photosynthate production (assuming free nutrient access through an established root system) by producing large leaves and/or large numbers of leaves (see Chapter 5). The sprouts are thus able to produce enough photosynthate to support their continued growth and an excess that can be stored as reserves. These reserves can be stored in both stems and roots, but because a greater proportion of the overall biomass of the plants I treated was in roots at the end of 2003, more TNC would be stored in the roots of treated plants than in the controls where TNC are stored in both stems and roots.

The overall health and size of root systems in this study were not evaluated beyond their carbohydrate concentrations. Although the majority of secondary roots were not injured by removing above-ground biomass, many fine roots and some secondary roots may not have survived the loss of above-ground stems and leaves. Fine roots are constantly dying and being replaced by new fine roots at a rate of up to 50% per year (Lauenroth & Gill 2003). Larger roots do not turn over at that rate, but can be affected by plant stress. Decreased carbohydrate reserves reduce the ability of roots to resist pathogens (Lauenroth & Gill 2003). Following repeated cutting of above-ground stems and the resulting depletion of TNC, it is likely that individual plant root systems declined. Although declines were not enough to impair sprout growth due to decreased access to resources, below-ground respiration costs would have decreased. This decrease in carbohydrate demand below-ground could contribute to the greater TNC in treated plants versus controls at the end of 2003. More research is necessary to evaluate the impact of above-ground stem removal on root systems and carbohydrate storage.

Invasive woody species are difficult to control due to their ability to sprout following cutting or burning. Treatments in the growing season are more successful than in the dormant season in reducing below-ground carbohydrate stores, although the degree of reduction depends on the species and the timing of treatments with respect to annual reserve depletion. I found that two years of annual growing-season treatments did not have a long-term impact on the six species I evaluated. Repeated cutting has eliminated *Gaylussacia baccata* (black huckleberry) after five years in a study at Cape Cod National Seashore (Patterson, unpublished data). To control the woody invasives in this study, a similar long-term commitment might achieve similar results.

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CHAPTER 5

CHANGES IN ABUNDANCE, HEIGHT, AND BIOMASS OF SIX INVASIVE

SHRUB SPECIES FOLLOWING CUT AND BURN TREATMENTS

Introduction

For many woody species, especially those of deciduous forests, the ability to

sprout is vital to persisting following disturbances (e.g. fires, wind storms, herbivory) that

injure or kill above-ground stems (Bond & Midgley 2001). Sprouting contributes to the

difficulty that land managers have in trying to eliminate invasive woody species from

natural vegetation. Cut, burn, and herbicide treatments as well as biocontrol agents

(alone or in combination) are often successful at killing above-ground stems, but root

systems remain intact and the plants resprout. Sprouts arise from roots, rhizomes,

stumps, or even stems by using the carbohydrate and nutrient reserves within the existing

root system. Growth rates can be high, as these sprouts quickly attain the stature and leaf

area necessary to meet the energy demands of the root system as well as their growing

stems. Knowledge of the ability of woody plants to sprout is available for coppiced trees

(Del Tredici 2001, Landhausser & Lieffers 2002, Frey *et al.* 2003) and a few shrubs

(Wildy & Pate 2002), but not for invasive shrubs following control efforts.

Plant species vary in their ability to sprout depending on their growth form, life

history stage, and adaptation to disturbances (Bond & Midgley 2001). Most conifer tree

species do not sprout, whereas most shrubs – both deciduous and evergreen - do. In general woody species can be divided into two categories according to their ability to survive disturbance: sprouters and seeders. Resource allocation patterns differ between these types: sprouters generally allocate more carbohydrates to reserves, whereas seeders have higher growth rates, reach reproductive maturity sooner, produce more and longer-lived seeds, and have greater seedling survival (Bond & Midgley 2001). Carbohydrates are stored in a variety of plant organs including stems, fine and coarse roots, foliage, fruits, and buds (Cook 1966, Kozlowski 1971, Kozlowski 1992). Species that sprout store more carbohydrates in roots (at the expense of accumulation of above-ground biomass) than species that rely on abundant seed production (Bowen & Pate 1993). Successful recovery following disturbance requires adequate carbohydrate reserves. A study of the shrub *Stirlingia latifolia* reported a 50-75% reduction in root reserves following fire (Bowen & Pate 1993). In deciduous species, carbohydrate reserves fluctuate during the year with a natural cycle of depletion at leaf-out and replenishment during the growing season. Therefore, the growth and vigor of sprouts can be influenced by when the disturbance occurs and the amount of carbohydrates stored at that time (Del Tredici 2001, Landhausser & Lieffers 2002). By timing treatments to times when reserves are low, subsequent sprouting is diminished, and follow-up treatments contribute to a continued decline in overall vigor if done before TNC are replenished.

The health and size of a root system, along with the amount of stored carbohydrates, are important to the successful production of sprouts. When the above-ground biomass of a woody plant is removed, its root system is left without the support of

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the necessary leaf area to satisfy its respiratory demands (DesRochers & Lieffers 2001,

Landhausser & Lieffers 2002). So quick growth of sprouts is crucial to the recovery of

adequate leaf area to maintain the below-ground biomass. After studying the below-

ground response of *Populus tremuloides* saplings following cutting, DesRochers and

Lieffers (2001) estimated that at least 20% of the root biomass was lost prior to

successful establishment of suckers (i.e. sprouts from the roots). Root systems can

experience even greater die-back if carbohydrate reserves are low or if the plants are not

able to produce large enough sprouts to support the roots (Landhausser & Lieffers 2002).

Chapter 4 discusses how different cutting treatments affect the concentration of

carbohydrate reserves in the roots of six invasive shrubs. In this chapter, I present the

effect that treatments and the resulting low TNC have on the growth of sprouts.

Methods

Seven invasive shrub species (two native and five non-native) were studied at

three locations (Figure 2-1): *Cornus racemosa*, *Rhamnus cathartica*, and *Rosa multiflora*

at the Montezuma National Wildlife Refuge, Seneca Falls, NY; *Berberis thunbergii* and

Lonicera morrowii under closed canopy forests in The Nature Conservancy's preserves

in Sheffield, Massachusetts; and the woody vine *Smilax rotundifolia* and the leguminous

shrub *Cytisus scoparius* in coastal grasslands on Naushon Island, Gosnold, MA. See

Chapter 2 for more detailed species and site descriptions.

At each site four 0.2 ha (40 m x 40 m) plots were located in areas with similar

overstory and understory vegetation and treated as described in Chapter 4 (Table 5-1).

An additional set of four plots was established at Naushon Island to study *Cytisus scoparius*.

The cover of the invasive species within each plot was determined using point-intercept sampling (Mueller-Dombois & Ellenberg 1974). Approximately 300 points were distributed on a 2 x 2 meter grid (except for pre-treatment sampling of *Smilax* which used a 4 x 2 m grid). Presence was recorded at each grid point and cover was calculated as the percent of points that intersected a species. I sampled all plots (except the Montezuma NWR Lay Road plot #3) in 2001 prior to application of treatments (Table5-1). In 2002 and 2003 all plots were re-sampled to determine change in cover following treatments. Treated plots were allowed to grow for at least three months before re-sampling.

To determine above-ground biomass of target species in the treatment plots, I harvested sprouts from three-to-five 40 x 40 cm subplots which were randomly placed in each of the treatment plots at all of the sites except Clark Ridge at Montezuma NWR (due to time constraints) and the *Cytisus* plots at Naushon (as this species did not readily sprout). Sprouts were not harvested from untreated plots. Sprouts were harvested for *Cornus* and *Rhamnus* at Lay Road (Montezuma NWR), *Berberis* at Bartholomew, *Lonicera* and *Berberis* at Bear Rock Stream, and *Smilax* at Naushon. Harvested sprouts were brought back to the lab, dried at 70°C until they reached a constant weight and divided into leaf and stem fractions. The heights of individual sprouts and the number of sprouts within each plot were also recorded (except for the *Smilax* plots due to deer

Table 5-1. Treatment protocols and point-intercept (PI) sampling dates.

Plot	2001 PI sampling	2001 treatments	2002 PI sampling	2002 treatments	2003 treatments	2003 PI sampling
Montezuma NWR – Lay Road – Cornus, Rhamnus						
Control	8/15	-	8/20	-	-	7/9
Mow/burn	6/18	Mow 6/23 Burn 8/24	ND	Mow 6/13 Mow 7/25	-	7/7
Cut/burn	ND	Cut 7/16 Burn 8/24	6/18	Mow 7/25	-	7/8
Mow-only	6/19	Mow 6/23	6/19	Mow 7/25	-	7/21
Dormant	8/16	-	8/21	Cut 4/24	Burn 4/25	7/22
Montezuma NWR – Clark Ridge – Cornus, Rhamnus, Rosa						
Cut-twice	6/19	Cut 7/13	7/17	Cut 8/14	-	7/24
Control	8/13	-	8/14	-	-	8/12
Dormant	8/14	-	8/20	Cut 4/23	-	7/23
Cut-once	6/19	Cut 7/17	7/18	-	-	8/13
Bartholomew Property – Berkshires – Berberis						
Dormant	7/27	-	8/16	Burn 4/19	-	8/7
Control	7/6	-	7/2	-	-	8/8
Cut/burn	7/5	Cut 7/6 Burn 11/18	6/24	Cut 7/25	-	8/7
Cut-only	6/15	Cut 7/6	6/24	Cut 7/25	-	8/7
Bear Rock Stream Property – Berkshires – Lonicera, Berberis						
Control	7/31	-	8/23	-	-	8/22
Cut/burn	7/3	Cut 7/10 Burn 11/18	6/10	Cut 6/13 Cut 7/24	-	6/30
Dormant	8/7	-	7/9	Cut 4/12	-	8/19
Cut-only	7/9	Cut 7/10	6/11	Cut 6/13 Cut 7/24	-	7/1
Naushon Island – Smilax						
Cut/burn	6/6	Cut 6/28 Burn 8/2	7/12	Cut 8/6	-	9/24
Dormant	8/28	-	7/10	Burn 4/5	-	9/25
Cut-only	6/27	Cut 6/29	7/11	Cut 8/6	-	9/24
Control	8/28	-	8/5	-	-	6/25
Naushon Island – Cytisus						
Cut/burn	6/26	Cut 6/28 Burn 8/2	7/10	-	-	6/10
Dormant	8/27	-	7/12	4/5	-	6/11
Cut-only	6/26	Cut 7/20	7/11	-	-	6/11
Control	8/27	-	8/6	-	-	6/26

browse of the sprouts). Sprouts for all plots at a site were sampled in late summer 2003

as follows: Montezuma NWR Lay Road – August 11(mow/burn & cut/burn) and 14 (cut

only & spring cut/burn); Bartholomew Property Berkshires – August 20; Bear Rock

Stream Property Berkshires – September 21; Naushon Island – September 25.

Root samples were collected pre- and post-treatment to determine the

concentration of total non-structural carbohydrates (TNC) in the study species. See

Chapter 4 for a detailed description of collection and analysis methods.

Results

Heights of sprouts differed depending on species, treatment type, and site

location. In general dormant-season-treated plots had taller sprouts by late summer 2003

than growing-season-treated plots (Figure 5-1), and estimated growth rates were 150-

1000% greater in the dormant-season-treated plants compared to the highest growing-

season treatment (Table 5-2). This was true for all species sampled except *Berberis* at the

Bartholomew site. In this case, the repeatedly cut plot had taller, although not

significantly (the 95% confidence intervals overlapped), sprouts at the time of harvest

(Figure 5-1) than those of the dormant plot. The dormant plot at this site was, however,

actually treated following leaf-out of *Berberis* so it can be considered a single growing-

season treatment. Although some of the height difference may have been due to the

differential amount of growing time since last treatment (Table 5-3), approximate sprout

growth rates indicate that dormant-season-treated plants grew much more quickly. In

fact, for *Cornus* and *Rhamnus* the dormant-plot sprouts were more than double the height

of sprouts on the other treatments despite the fact that the dormant plot was treated only

four months before the samples were collected and sprouts on the growing-season plots

had more than a year to grow before sampling. The growing-season treatments, cut/burn

vs. mow/burn vs. multiple cut, were generally similar in their sprout heights (overlapping

95% confidence intervals) and growth rates for *Cornus*, *Berberis* at Bear Rock Stream,

and *Lonicera*. In the cut plot for *Rhamnus*, however, heights and growth rates were

greater than in the other growing-season plots, but much shorter than the dormant-season

plot. The three *Berberis* plots at Bartholomew were all treated in the growing season,

although one dormant treatment was planned. The sprouts on the cut/burn plots were

significantly shorter than on the other treatments for *Berberis*.

Table 5-2. Approximate sprout biomass growth rates (mg m^{-2} d^{-1}) following treatments.
Growth rates based on average length of growing season for each site – Montezuma
NWR 185 days, Sheffield (Bartholomew & Bear Rock) 130 days, and Naushon Island
185 days.

Species/site	Dormant	Cut/cut	Cut/burn	Mow/burn
Cornus – Montezuma	2889	394	281	234
Rhamnus – Montezuma	2765	1724	828	659
Berberis - Bartholomew	187	370	141	-
Berberis – Bear Rock	974	73	89	-
Lonicera – Bear Rock	1415	228	232	-
Smilax - Naushon	1423	689	394	-
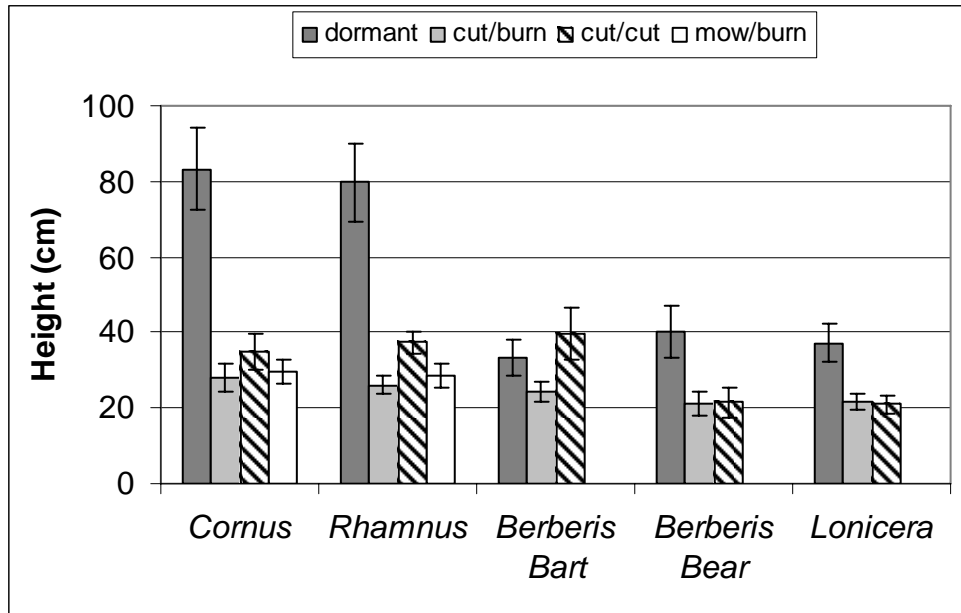
Figure 5-1. Average height (cm) of sprouts harvested at the end of the 2003 growing season. Error bars are 95% confidence intervals. All plots except the "dormant" treatment were treated during the growing season. Bart – Bartholomew site, Bear – Bear Rock Stream site.

The small harvest plot size (0.16 m^2) resulted in large variation in estimates of sprout density (Figure 5-2). Although the dormant-season plots tended to be taller, generally they had lower sprout densities compared to the growing-season-treated plots although these differences are not significant (Figure 5-2). Except for the dormant-season treatment, all *Rhamnus* treatments had higher sprout densities than the other species.

Table 5-3. Date of last treatment prior to harvest and date of harvest of samples for height, density, and biomass of sprouts from 40 cm x 40 cm randomly placed quadrats.

Plot #	Treatments	Date of last treatment	Destructive harvest
Montezuma NWR – Lay Road			
Lay - 1	Control	-	-
Lay - 2	Mow, burn, mow, mow	July 25, 2002	August 11, 2003
Lay - 3	Cut, burn, mow	July 25, 2002	August 11, 2003
Lay - 4	Mow, mow	July 25, 2002	August 14, 2003
Lay - 5	Spring cut, spring burn	April 25, 2003	August 14, 2003
Bartholomew Property – Berkshires			
Bart - 1	Spring burn	April 19, 2002	August 20, 2003
Bart - 2	Control	-	-
Bart - 3	Cut, burn, cut	July 25, 2002	August 20, 2003
Bart - 4	Cut, cut	July 25, 2002	August 20, 2003
Bear Rock Stream Property – Berkshires			
Bear - 1	Control	-	-
Bear - 2	Cut, burn, cut, cut	July 24, 2002	September 21, 2003
Bear - 3	Spring cut	April 12, 2002	September 21, 2003
Bear - 4	Cut, cut, cut	July 24, 2002	September 21, 2003
Naushon Island			
Nau - 5	Cut, burn, cut	August 6, 2002	September 25, 2003
Nau - 6	Cut, cut	August 6, 2002	September 25, 2003
Nau - 7	Spring burn	April 5, 2002	September 25, 2003
Nau - 8	Control	-	-
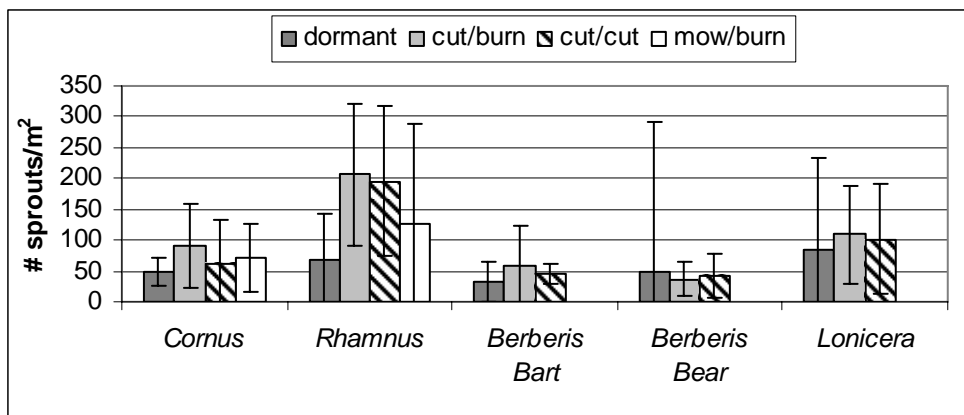
Figure 5-2. Density of sprouts (#/m^2) for plots sampled at the end of the 2003 growing season.. Error bars are 95% confidence intervals. All plots except the "dormant" treatment were treated during the growing season. Bart – Bartholomew site, Bear – Bear Rock Stream site.

Although confidence intervals were generally large and overlapping, biomass tended to be greater in the dormant-season-treated plots and was significantly so for *Lonicera* (Figure 5-3). This trend was true for stem biomass, leaf biomass, and the two combined. For *Cornus* and *Smilax,* at least one growing-season-treated plot had significantly less biomass than the dormant-season-treated plot. The difference in biomass between the different treatments is related more to the number of treatments and when they were applied than the amount of growing time since last treatment. This is especially noticeable for *Cornus* where the dormant-season-treated sprouts weighed more than three times those of the growing-season-treated sprouts even though they only grew for four months before harvest compared to more than one year (Figure 5-3). There was an inverse relationship between number of growing-season treatments and biomass for *Cornus*, *Berberis*, *Lonicera*, and *Smilax* combined (Figure 5-4, 5-5). *Rhamnus* also follows that trend although it was not included in the combined data set as its sprout biomass was much greater than the other species.
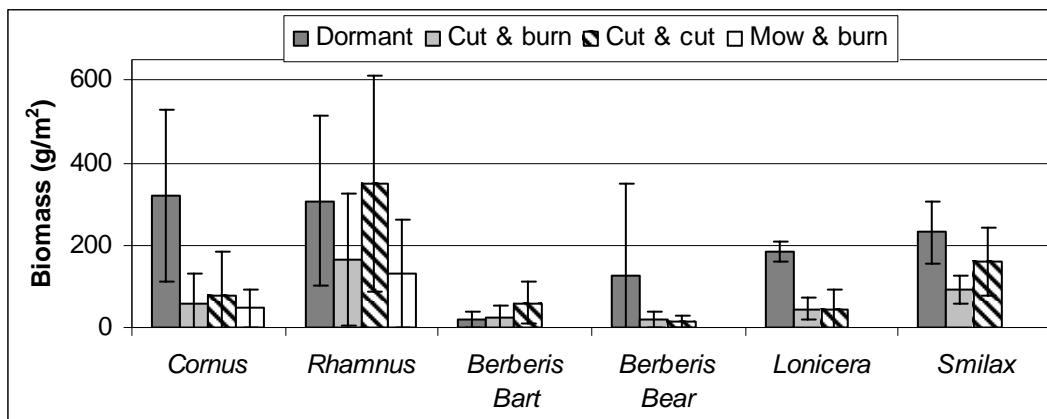
Figure 5-3. Biomass (g/m^2) of sprouts for plots sampled at the end of the 2003 growing season. Error bars are 95% confidence intervals. All plots except the "dormant" treatment were treated during the growing season. Bart – Bartholomew site, Bear – Bear Rock Stream site.
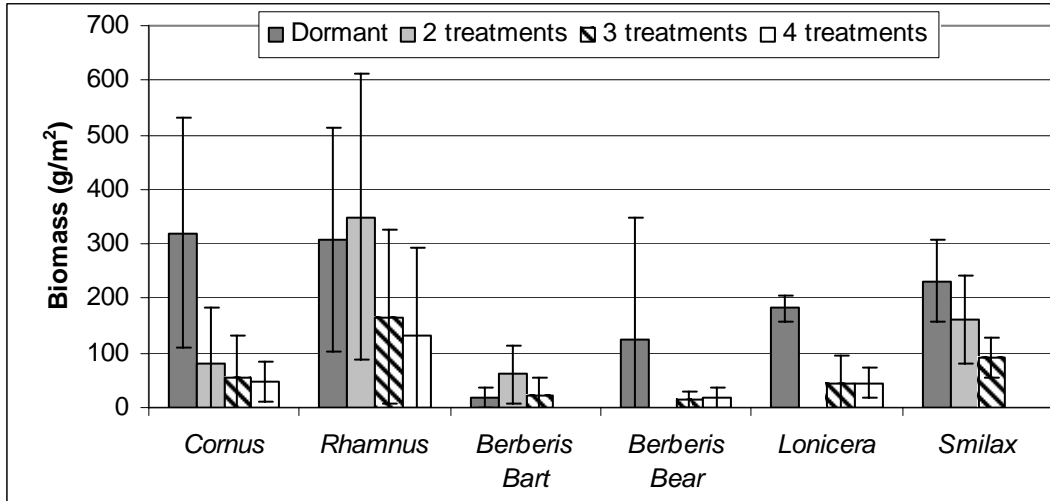
Figure 5-4. Biomass (g/m^2) of sprouts (+/- 95% confidence intervals) for plots sampled at the end of the 2003 growing season.. All plots except the "dormant" treatment were treated during the growing season. Bart – Bartholomew site, Bear – Bear Rock Stream site.
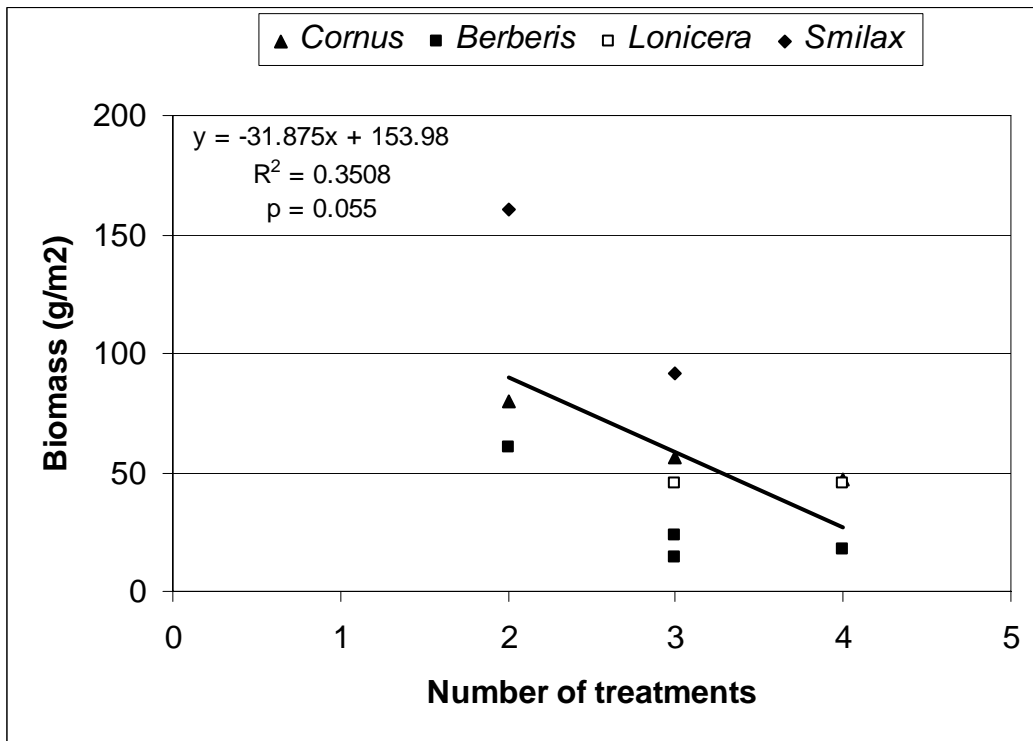
Figure 5-5. The relationship between number of growing-season treatments and sprout biomass (g/m^2) for plots sampled at the end of the 2003 growing season..

Biomass was positively related to the concentration of total non-structural carbohydrates for *Cornus*, *Rhamnus*, *Lonicera*, and *Smilax* combined (Figure 5-6). Sprout height was positively related to TNC as well for *Cornus*, *Rhamnus*, and *Lonicera* combined (Figure 5-7). *Berberis* sprout biomass and height were much lower than those of the other species and were not positively related to TNC.
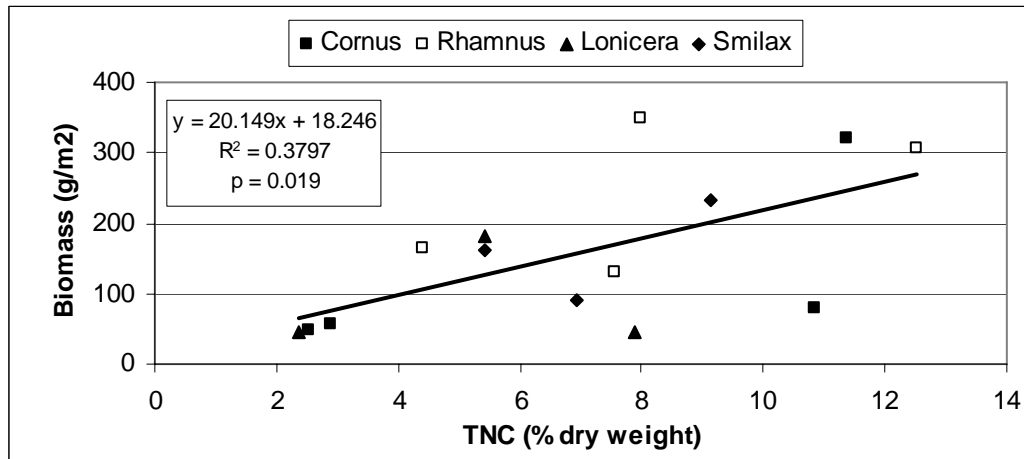
Figure 5-6. Relationship of total non-structural carbohydrates (TNC) prior to treatment and the biomass of sprouts harvested in late summer 2003 among treated plots.
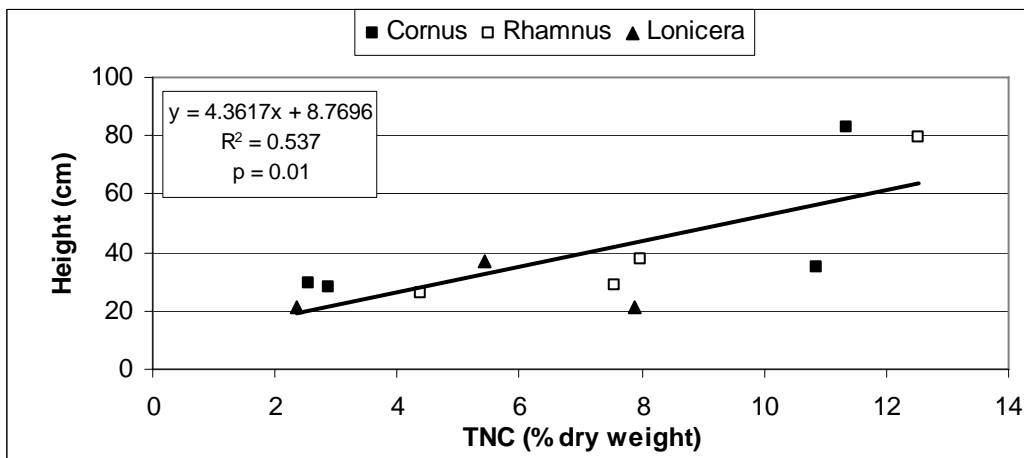
Figure 5-7. Concentration of total non-structural carbohydrates (TNC) prior to treatment and the average height of sprouts harvested in late summer 2003.

Prior to treatments in 2001, *Cornus* dominated the plots at the Lay Road site at Montezuma NWR (70-75% cover), whereas *Rhamnus* had less cover (3-9%, Figure 5-8). *Cornus* also dominated at Clark Ridge (67-86% cover) in all but one plot (39%), but *Rhamnus* was more abundant (6-17% cover) there than Lay Road, perhaps due to its height and age. Thickets at Clark Ridge were generally taller than at Lay Road. Initial cutting treatments in 2001 (or 2002 for the dormant-season treatment) eliminated all live above-ground stems, except for small stumps. By June 2002, *Cornus* at Lay Road had recovered to 20 and 44% for cut/burn and mow-only plots respectively as sprouts grew from stumps and suckers from roots prior to the application of 2002 treatments. *Rhamnus* similarly declined to less than half its original cover following all treatments. At Clark Ridge *Cornus* and *Rhamnus* cover declined following growing-season treatments but not in the dormant-season-treated *Cornus*. At Lay Road, dormant-season treatments were applied twice, first in the spring of 2002 with a cut treatment and then a burn treatment in spring on 2003, but dormant treatments at Clark Ridge were only applied once in the spring of 2002 (a cut treatment). At the end of 2003, with one full growing season without treatments, the cover of *Cornus* at Lay Road remained lower than before any treatment and in fact decreased (though not significantly) between 2002 and 2003. Cover of *Rhamnus* did not change between 2002 and 2003.
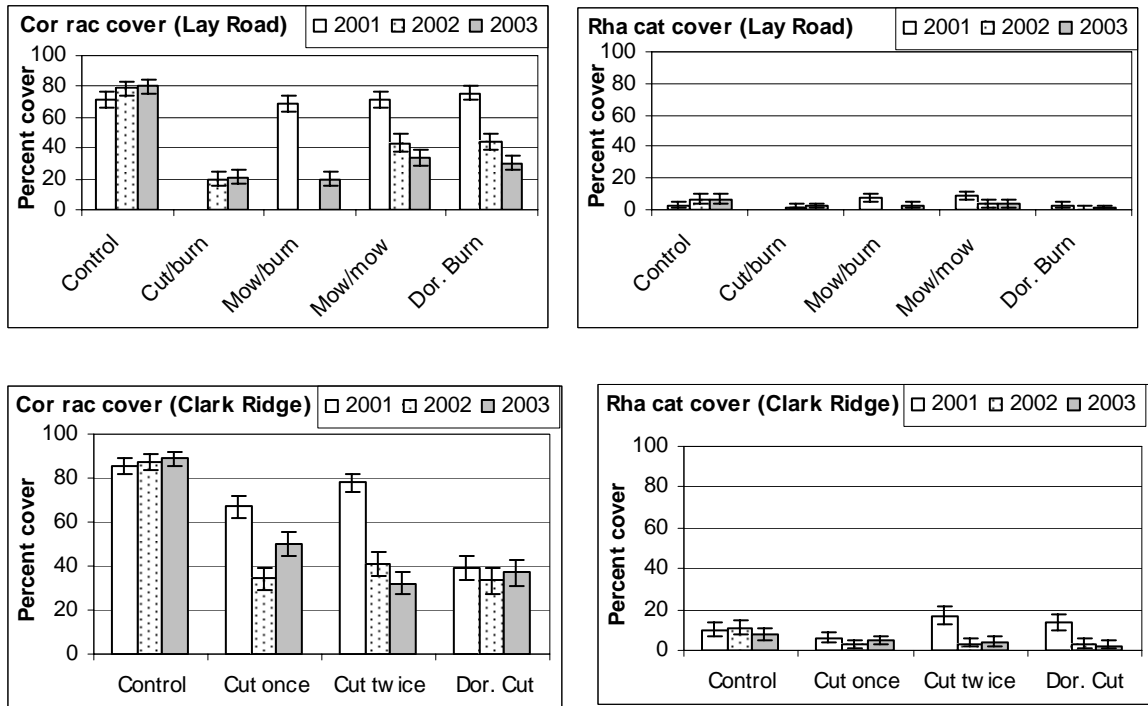
Figure 5-8. Percent cover of *Cornus racemosa* and *Rhamnus cathartica* at Montezuma NWR plots. Error bars indicate 95% confidence intervals.

The cover of *Rosa*, *Berberis*, *Lonicera*, and *Smilax* all declined following initial treatments and then recovered partially with the formation of sprouts (Figures 5-9, 5-10). At Clark Ridge pre-treatment *Rosa* cover of 5-10% was reduced to 0-2% after cutting, regardless of season of treatment. Recovery following treatments was slow, with *Rosa* cover remaining less than 3% in treated plots by mid-late summer 2003.

Berberis occurred at both sites in the Berkshires. At the upland site (Bartholomew), *Berberis* pre-treatment cover was approximately 80% in three of the four plots (the dormant-burn plot had 30% initial cover, Figure 5-9). All treatments significantly reduced this species' cover through 2003 with a decrease in cover of nearly

90% in treatments that included a burn regardless of season (from 83% and 31% in 2001

to 5% and 3% in 2003 for growing-season and dormant-season-burn plots respectively)

and 75% in the cut plot (from 85% in 2001 to 23% in 2003). At the wetland site (Bear

Rock Stream), *Berberis* cover declined following treatments, with the greatest declines in

growing-season-treated plots. *Lonicera* pre-treatment cover was close to 50% or greater

in all Bear Rock Stream plots, except the dormant-treated plot (23% cover, Figure 5-9).

By 2003 sprout cover remained ≤ 50% of the original cover in the growing-season-

treated plots, but was reduced only 25% in the dormant-treated plots.
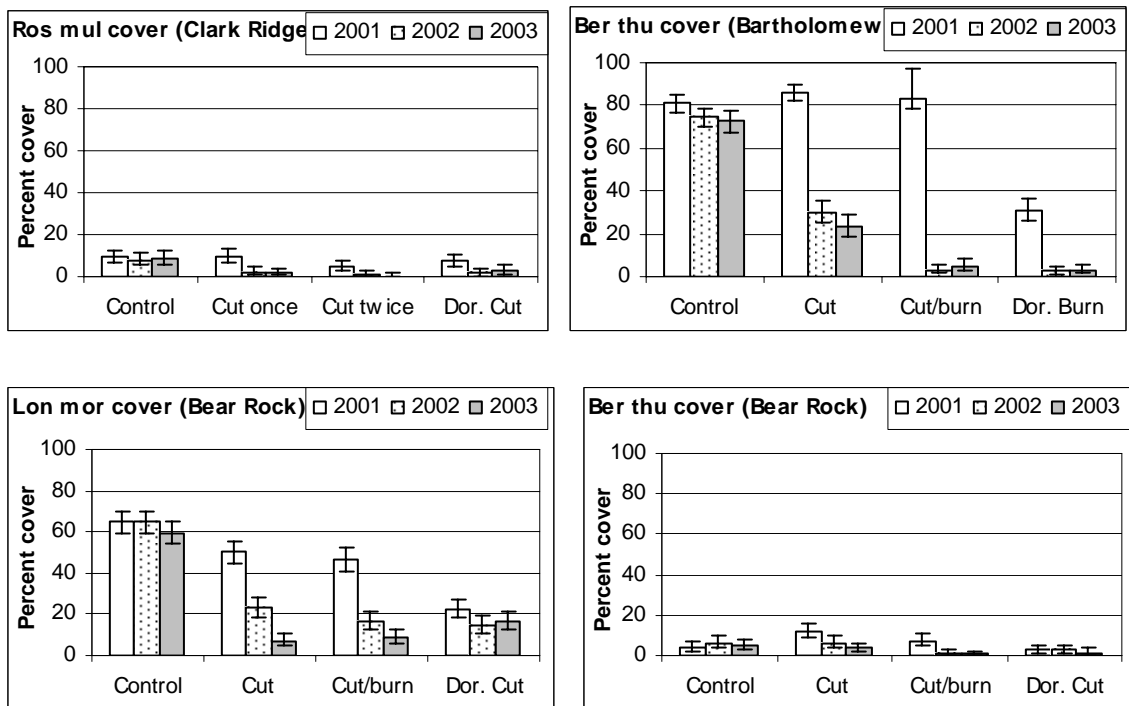
Figure 5-9. Percent cover of *Rosa multiflora, Berberis thunbergii,* and *Lonicera morrowii*. Error bars indicate 95% confidence intervals.

Pre-treatment *Smilax* cover was 90-100% in three out of four plots but only 60% in the cut/burn plot (Figure 5-10). All treatments decreased cover by at least 50%, but the dormant-season-burned plot recovered the most by 2003. Although *Cytisus* did not effectively sprout, pre-treatment cover (40-64%) recovered to nearly 20-25% cover from seedlings in the growing-season-treated plots (Figure 5-10). Weak sprouts formed in the dormant-season-burned plot, but there was almost no recovery following the treatment as the sprouts did not survive and only a few seedlings established. Cover in the untreated control plot decreased significantly in 2003, likely the result of a long, cold period the winter before (as *Cytisus* stems die-back in severe winters), but the cover of seedlings increased during the same period.
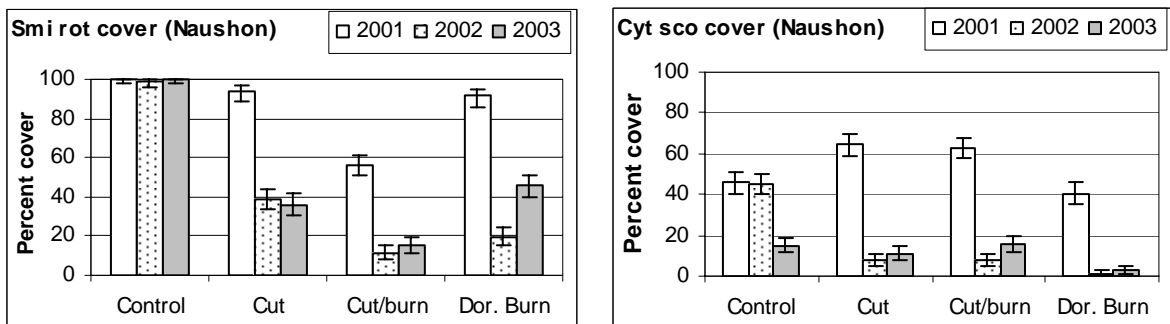
Figure 5-10. Percent cover of *Smilax rotundifolia* and *Cytisus scoparius* in Naushon Island plots. Error bars indicate 95% confidence intervals.

Discussion

All species included in this study (except *Cytisus*) produced sprouts following stem removal; whether through cutting or burning, in the dormant or growing season.

Sprout initiation and growth can produce adequate leaf area to support the cut (or burned) plant's existing root system, thereby contributing to the resilience of the plant at a location. Once the sprouts produce enough photosynthate to support the respiration requirements of the roots as well as their own continued growth, root carbohydrate reserves are replenished. Although root biomass may decrease following removal of above-ground stems, most of the root system can be preserved if sprout growth is rapid (Landhausser & Lieffers 2002). The size and vigor of sprouts of deciduous trees are related to the amount of root reserves at the time of cutting (Kays & Canham 1991, Landhausser & Lieffers 2002, Frey *et al.* 2003), and this relationship held for the shrubs I studied. Heights and biomass of the shrub sprouts were positively related to the concentration of underground root reserves (Figures 5-5 & 5-6); and the growth of sprouts led to partial recovery of cover following the treatments.

Timing treatments to periods when TNC reserves were low (i.e. during the early growing season or following resprouting) resulted in reduced sprout growth. This result is comparable to that observed following the cutting of tree species such as aspen, birch, maple, ash, and cherry (Kays & Canham 1991, Landhausser & Lieffers 2002). For the three-year period of this study, sprout growth following growing-season treatments was less than that following dormant treatments, even when given more time to grow following treatment. For *Cornus* and *Rhamnus*, the results are striking, with sprout growth being much greater in the dormant-treated plots four months after treatment compared to growing-season-treated plots where plants had more than a year to recover (at least double the amount of "growing season" time; Figure 5-1). For other species,

although their heights and biomass differed less, the growing-season-treated plants did not recover as quickly as plants treated in the dormant season. For *Berberis* and *Lonicera* at the Bear Rock Stream Site, the dormant-season-treated plants had more than twice the biomass of the growing-season-treated plants; a result that cannot be explained solely by the difference in amount of growing time before harvest. For *Berberis* at the Bartholomew property, however, there was a different result, with plants treated in the dormant-season burn producing less biomass than those cut during the growing season. Although the treatment was attempted during the dormant season (April), the *Berberis* plants had already leafed-out (and root reserves were low – see Chapter 4), so this was, in fact, an early growing-season treatment. Low reserves at the time of treatment resulted in less biomass production than in the growing-season treatment where plants had partially replenished their reserves at the time of treatment.

In general, the more treatments that were applied following an initial growing-season treatment, the less sprout biomass was produced (Figures 5-4 & 5-5). Although 95% confidence intervals calculated for biomass overlapped for all but *Smilax* when comparing growing-season treatments, the trend of less biomass at time of harvest with increasing number of treatments is significant, with the exception of the two species that occurred at the Bear Rock Stream site (*Lonicera* and *Berberis*). For the other species, the greatest difference is between plots receiving 2 versus 3 treatments. Those that received a fourth treatment produced biomass similar in amount to those receiving three. The Bear Rock Stream plots follow this pattern, although I did not apply a two-treatment regime at that site.

The slowing of the decline in sprout biomass produced following multiple treatments may indicate a loss of root biomass as well as a decrease in TNC. The sprouts may not produce enough photosynthate to meet both above- and below-ground growth and respiratory requirements which results in root decline. The decrease in root biomass along with a decreasing concentration of stored reserves results in less vigorous sprouting following continued treatments.

In addition to a difference in sprouting response due to timing or numbers of treatments, there is species-to-species variation which depends on where sprouts originate (how many buds were damaged by the treatment), the age and size of the individuals, and in the amount of reserves required for growing new sprouts (Del Tredici 2001). *Cornus*, *Smilax*, and *Rhamnus* generally produced more biomass following all treatments than the other species in the study. *Cornus* and *Smilax* are both clonal species, and therefore may have been able to acquire TNC from portions of the clone outside of the treatment plots. The amount of *Smilax* biomass is especially impressive, as the sprouts were consistently grazed by deer requiring the plants to continually sprout new foliage and stems through the 2003 growing season. The large sprouting response of *Rhamnus* might be due to the greater below-ground biomass of this species compared to others I studied. Although I did not measure it directly, I assume that the *Rhamnus* plants had larger root mass per stem based on their larger stems and root diameters than other species I studied (Richburg, pers. obs.). This additional root mass, along with the larger stumps, may explain why *Rhamnus* treated in the growing season was able to produce many more sprouts and more biomass than *Cornus*, even though their TNC concentrations were both

depleted. The amount of below-ground carbohydrate reserves is influenced not only by the concentration of reserves in the roots, but also in the amount of root material. The large root system of larger above-ground stems can produce more sprouts than the smaller root system of smaller plants (Kramer & Kozlowski 1960). It is important to note, however, that the above-ground sprouts may not be able to support the entire biomass underground resulting in some decrease in live underground biomass (Landhausser & Lieffers 2002, Lauenroth & Gill 2003). In addition, repeated treatments likely further reduce root biomass, as smaller sprouts are not able to support the existing root system resulting in death of some medium and large roots (Wildy & Pate 2002).

Although sprout biomass and height differed among treatments, the sprout densities were generally similar across treatment types. Similar responses have occurred with other woody tree and shrub species, perhaps due to sprout initiation being due more to environmental conditions than concentrations of carbohydrates (Wildy & Pate 2002, Frey *et al.* 2003). Soil temperature and moisture content following disturbance are the most important factors in controlling sprout initiation, whereas carbohydrate reserves are more important to sprout growth (Frey *et al.* 2003).

For land managers interested in eliminating invasive species, sprout growth is discouraging. Although the cover of the species declines dramatically following treatments as mature, large stems are eliminated, the production of healthy vigorous sprouts ultimately leads to recovery to pretreatment conditions. None of the treatment regimes applied in this study successfully eliminated the species (although *Cytisus*

persisted only with seedlings), and in some cases there was a rapid recovery of cover

following sprout growth. In some plots sprout cover reached more than 70% of pre-

treatment cover within two years. This is especially evident following dormant-season

treatments or single growing-season treatments. Continuing to treat these species beyond

two consecutive growing seasons would further stress the existing root system resulting

in decreased sprouting, death of additional roots, and increased susceptibility to disease.

For the species in this study, more than two growing seasons of periodic treatments are

necessary to eliminate them, although additional research is necessary to determine just

how many treatments and years would be required.

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CHAPTER 6

CHANGE IN PLANT SPECIES COMPOSITION AND ABUNDANCE FOLLOWING

TREATMENT OF INVASIVE SHRUBS WITH CUTTING AND PRESCRIBED FIRE

<u>Introduction</u>

Plant invasions are threatening rare species and natural communities worldwide.

Their impacts on biodiversity are considered second only to habitat destruction and

fragmentation (Randall 1996, Westbrooks 1998). Invasive plants influence vegetation

composition and other species' abundance directly through competition for resources,

and indirectly through the alteration of natural processes (Hobbs & Humphries 1995,

Myers & Bazely 2003). The effects of these plants are often determined by comparing

invaded areas with uninvaded counterparts (Hutchinson & Vankat 1997, Kourtev *et al.*

1999, Collier *et al.* 2002, Frappier *et al.* 2003) and inferring that differences are due to

the invader. Experimental studies that involve growing native and exotic invasive

species together, whether in the lab or in the field, have evaluated the effects of invasives

on the survival and growth of native species (Schweitzer & Larson 1999, Gould &

Gorchov 2000). Few data are available on the effects of an invader recorded during the

process of invasion (Fike & Niering 1999, Meiners *et al.* 2001, Briggs *et al.* 2002).

In forests and grasslands, aggressive invasive shrubs can out-compete other plants

for vital resources such as light, water, and nutrients. Species richness, seedling density,

and abundance of native species are diminished beneath these invaders, which include, in the northeastern United States, *Lonicera maackii*, *L. tatartica*, and *Rhamnus frangula* (Woods 1993, Collier *et al.* 2002, Frappier *et al.* 2003). The length of the invasion influences species richness and density with longer invasions resulting in increased cover of the invader and decreased richness (Woods 1993, Hutchinson & Vankat 1997, Collier *et al.* 2002, Frappier *et al.* 2003). In forests native tree seedlings may not survive beneath the invasive species, so the long-term stability of the forest community could be at risk (Woods 1993, Hutchinson & Vankat 1997, Collier *et al.* 2002). In the Northeast grassland species and communities are threatened by the invasion of native and non-native shrubs, vines, and trees. These areas, which historically were kept relatively free of woody species by burning, plowing, and/or grazing, are being invaded by woody species once abandoned. These invasions have resulted in changes in species richness and abundance of grassland species (Myster & Pickett 1992, Fike & Niering 1999, Meiners *et al.* 2002). Localized extinctions of uncommon plant species may occur in areas invaded by aggressive shrub species (Woods 1993, Collier *et al.* 2002).

As the problems associated with invasive plants are better understood, land managers are attempting to eradicate or limit the abundance of these species in natural systems (Hobbs & Humphries 1995, Westman 1990). In some cases, invasive plants are being removed with little knowledge of how their removal will impact the communities within which they occur (Hobbs & Humphries 1995, Westman 1990). It is essential that managers understand the impacts of the species invasions and their removal in order to prioritize which invasive problems to address given limited resources (Westman 1990).

Research is beginning to provide this information, although few studies have evaluated how a natural community responds once a dominant invasive species is controlled (Frappier *et al.* 2004). Here I report changes in vegetation composition and abundance following treatments to reduce the abundance and stature of five woody invasive species.

Methods

Five invasive shrub species were studied at three locations (Figure 2-1). *Cornus racemosa* dominated two old-field sites located at the Montezuma National Wildlife Refuge (NWR), Seneca Falls, NY. *Lonicera morrowii* and *Berberis thunbergii* occurred in forests in Sheffield, Massachusetts. *Smilax rotundifolia* and *Cytisus scoparius* dominate many hectares of coastal grassland on Naushon Island, Gosnold, MA.

At each location four 0.2 ha (40 m x 40 m) plots were established in areas with similar vegetation and randomly assigned to treatments as described in Chapter 4. In addition, a second set of four plots was established at Naushon to evaluate changes following *Cytisus* control (Table 6-1).

Table 6-1. Treatment protocol (all treatments were carried out in the summer unless specified otherwise).

Plot #	2001 treatments	2002 treatments	2003 treatments	Total # treatments
Montezuma NWR – Lay Road – Cornus racemosa				
Lay - 1	-	-	-	0 (control)
Lay - 2	Mow, burn	Mow, mow	-	4
Lay - 4	Mow	Mow	-	2
Lay - 5	-	Spring cut	Spring burn '03	2
Montezuma NWR – Clark Ridge – Cornus racemosa				
Clark - 1	Cut	Cut	-	2
Clark - 2	-	-	-	0 (control)
Clark - 3	-	Spring cut	-	1
Clark - 4	Cut	-	-	1
Bartholomew Property – Berkshires – Berberis thunbergii				
Bart - 1	-	Spring burn	-	1
Bart - 2	-	-	-	0 (control)
Bart - 3	Cut, burn	Cut	-	3
Bart - 4	Cut	Cut	-	2
Bear Rock Stream Property – Berkshires – Lonicera morrowii				
Bear - 1	-	-	-	0 (control)
Bear - 2	Cut, burn	Cut, cut	-	4
Bear - 3	-	Spring cut	-	1
Bear - 4	Cut	Cut, cut	-	3
Naushon Island – Cytisus plots 1-4, Smilax plots 5-8				
Nau - 1 & 5	Cut, burn	Cut (5 only)	-	2 or 3
Nau - 2 & 7	-	Spring burn	-	1
Nau - 3 & 6	Cut	Cut (6 only)	-	1 or 2
Nau - 4	-	-	-	0 (control)
Nau - 8	-	-	-	0 (control)

Plant community composition of each plot was determined using point-intercept

sampling as described in Chapter 5. Species within the plot, but that did not intersect a

point during sampling were noted along with a visual estimate of their cover for inclusion

in richness and cover calculations. Thus the entire plot became a relevé sample (Mueller-

Dombois & Ellenberg 1974). I sampled all plots in 2001 prior to application of

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treatments and in 2003 after treatments to determine differences in community composition. Each species was assigned to one of four growth forms for analysis – graminoid, herbaceous, shrub, or vine. Presence of vines within the plots was infrequent and results are not presented here.

Results

Growing-season treatments reduced cover of the dominant invasive species significantly (Table 6-2, see also Chapter 5), although four of the five species persisted at the sites by sprouting. *Cytisus*, unlike the others, produced only weak sprouts but reproduced prolifically from seed. Dormant-season treatments produced significant declines in cover for *Cornus* at Lay Road, *Berberis* at Bartholomew, and *Smilax* and *Cytisus* at Naushon. The Lay Road dormant-treatment plot was treated twice, first in April 2002 and then again in April 2003, unlike the single dormant treatments at the other sites. Although the dormant-treatment at Bartholomew was applied in mid-April before native species had leafed-out, *Berberis* had fully leafed-out so this treatment should be considered a growing-season treatment.

Table 6-2. Cover of the dominant invasive shrub before and after treatments. Significant differences (non-overlapping 95% confidence intervals) are bolded.

Site / plot	2001	2003
Lay Road (Montezuma NWR) - Cornus racemosa		
Lay 1 (control)	71	80
Lay 2 (mow/burn)	**69**	**20**
Lay 4 (mow)	**72**	**34**
Lay 5 (dormant cut/burn)	**76**	**30**
Clark Road (Montezuma NWR) - Cornus racemosa		
Clark 1 (cut twice)	**78**	**32**
Clark 2 (control)	86	89
Clark 3 (dormant cut)	39	37
Clark 4 (cut once)	**67**	**50**
Bartholomew Property (Berkshires) - Berberis thunbergii		
Bart 1 (dormant burn)	**31**	**3**
Bart 2 (control)	81	73
Bart 3 (cut/burn)	**83**	**5**
Bart 4 (cut)	**86**	**23**
Bear Rock Stream Property (Berkshires) - Lonicera morrowii		
Bear 1 (control)	65	60
Bear 2 (cut/burn)	**47**	**9**
Bear 3 (dormant cut)	23	16
Bear 4 (cut)	**50**	**7**
Naushon Island - Smilax rotundifolia		
Nau 5 (cut/burn)	**56**	**15**
Nau 6 (cut)	**94**	**36**
Nau 7 (dormant burn)	**91**	**45**
Nau 8 (control)	100	99
Naushon Island - Cytisus scoparius		
Nau 1 (cut/burn)	**63**	**15**
Nau 2 (dormant burn)	**40**	**2**
Nau 3 (cut)	**64**	**11**
Nau 4 (control)	**46**	**17**

Diversity of plant species varied among locations and habitat types. The Bear Rock Stream site in the Berkshires was the most diverse site prior to treatments in 2001. This wetland site had a partially open canopy that, along with calcium-rich groundwater, provided suitable habitat for over 100 plant species. The open fields of Montezuma

NWR (both Lay Road and Clark Ridge) had 85-90 species. The upland site in the Berkshires (Bartholomew) had close to 50 species under a closed deciduous canopy, whereas Naushon Island had the fewest species; only 15 among the 8 plots sampled. Following treatments, all plots either increased in richness or remained close to their pre-treatment levels (Table 6-3). The richness of treated plots at Montezuma NWR increased more than the other sites with an average of 60% more species in 2003 than 2001. There was no significant relationship between cover of invasive species and the change in richness following treatments, although there was an overall trend of increasing richness with decreasing invasive shrub cover.

Total shrub cover generally decreased significantly at all of the plots at each site following treatments (Figure 6-1). In 2001 each of the sites was dominated by the target shrub species (*Cornus*, *Berberis*, *Lonicera*, *Smilax*, or *Cytisus*). Following treatments in 2001 and 2002, the cover of these species declined contributing greatly to the overall decline in shrub cover. The dormant-treated plots at Clark Ridge and Bear Rock Stream, as well as the cut/burn plot at Bear Rock, decreased in total shrub cover although not significantly. At these sites, non-target shrubs were avoided where possible during treatments and this tempered the changes in total shrub cover.

Table 6-3. Species richness before (2001) and after treatments (2003).

Site / plot	2001	2003
Lay Road (Montezuma NWR) target species Cornus racemosa		
Lay 1 (control)	41	55
Lay 2 (mow/burn)	35	60
Lay 4 (mow)	32	57
Lay 5 (dormant cut/burn)	41	68
Clark Road (Montezuma NWR) target species Cornus racemosa		
Clark 1 (cut twice)	36	61
Clark 2 (control)	38	49
Clark 3 (dormant cut)	43	56
Clark 4 (cut once)	46	71
Bartholomew Property (Berkshires) target species Berberis thunbergii		
Bart 1 (dormant burn)	47	43
Bart 2 (control)	43	44
Bart 3 (cut/burn)	44	45
Bart 4 (cut)	32	27
Bear Rock Stream Property (Berkshires) target species Lonicera morrowii		
Bear 1 (control)	50	56
Bear 2 (cut/burn)	69	59
Bear 3 (dormant cut)	61	63
Bear 4 (cut)	60	59
Naushon Island target species Smilax rotundifolia		
Nau 5 (cut/burn)	11	11
Nau 6 (cut)	9	10
Nau 7 (dormant burn)	8	10
Nau 8 (control)	9	7
Naushon Island target species Cytisus scoparius		
Nau 1 (cut/burn)	4	9
Nau 2 (dormant burn)	6	9
Nau 3 (cut)	9	12
Nau 4 (control)	6	6
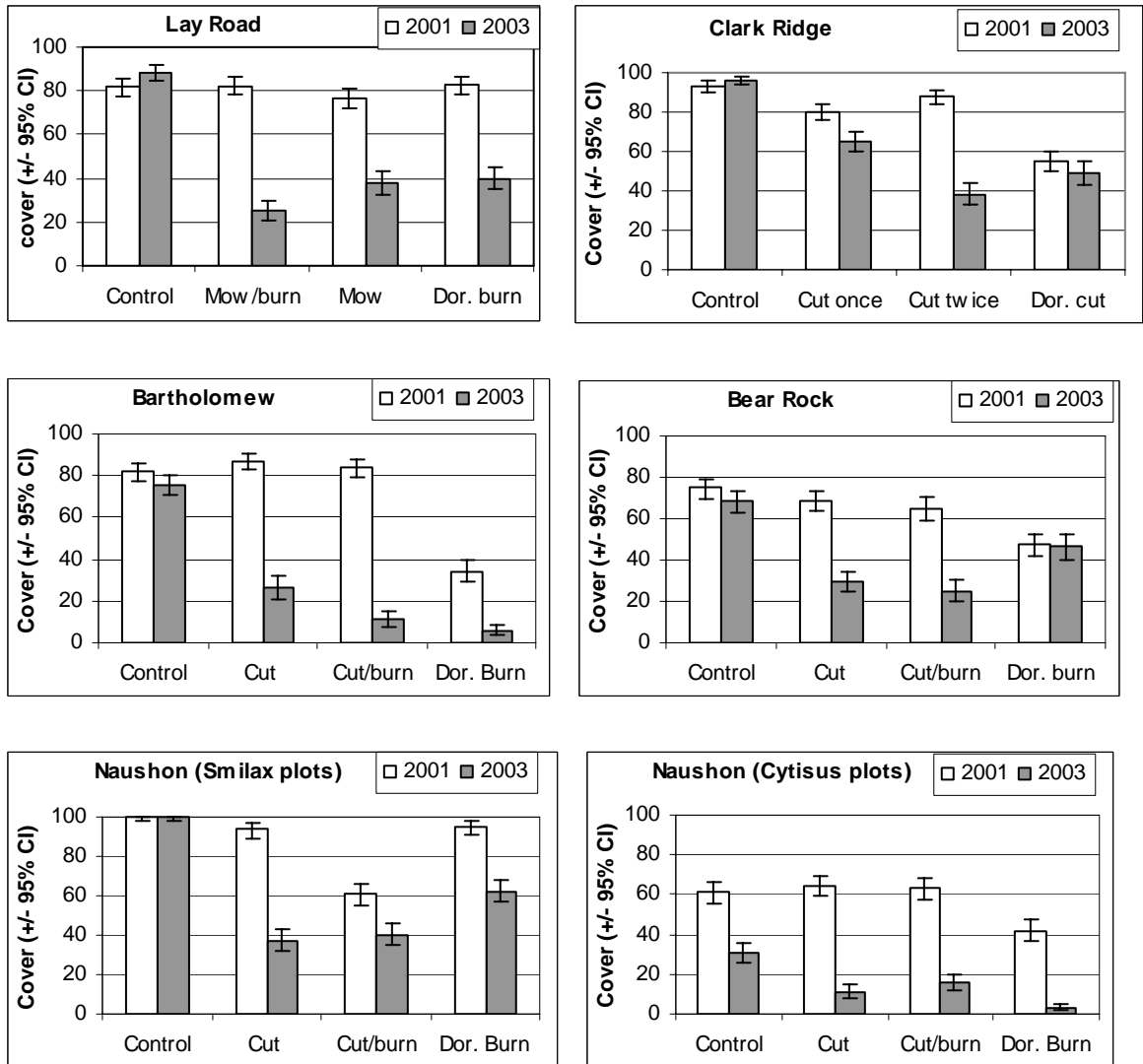
Figure 6-1. Shrub cover before (2001) and after (2003) treatments to control five invasive shrubs (Lay Road & Clark Ridge - *Cornus*, Bartholomew - *Berberis*, Bear Rock - *Lonicera*, Naushon - *Smilax & Cytisus*).

Herbaceous and graminoid species were affected by the treatments, although the effects varied depending on site, their pre-treatment cover, and treatment type. At the Montezuma NWR sites (Figure 6-2), herb and graminoid cover each exceeded 50% before treatments and either increased or remained the same following treatments. Cover of herbs increased significantly following the mow/burn-growing-season and dormant-

season treatments at Lay Road. Graminoid cover increased significantly at Clark Ridge

following treatments (but decreased in the control) and in the mow/burn-treated plot at

Lay Road.

Figure 6-2. Graminoid and herb cover (and 95% confidence intervals) before (2001) and
after (2003) treatments to control *Cornus racemosa* at two sites at Montezuma NWR.

Herb and graminoid cover did not change significantly at the Berkshire sites,

except for an increase of graminoids in the Bear Rock cut plot (Figure 6-3). On Naushon

graminoids significantly increased following treatments of *Smilax* invaded plots, whereas

they decreased in the *Cytisus* burned plots regardless of season of burn (Figure 6-4).

Herbaceous cover was small before and after treatments on Naushon, and only

significantly changed in the growing-season-cut plot.

Figure 6-3. Graminoid and herb cover (and 95% confidence intervals) before (2001) and after (2003) treatments to control *Berberis thunbergii* at Bartholomew and *Lonicera morrowii* at Bear Rock, Sheffield Nature Conservancy Preserves.
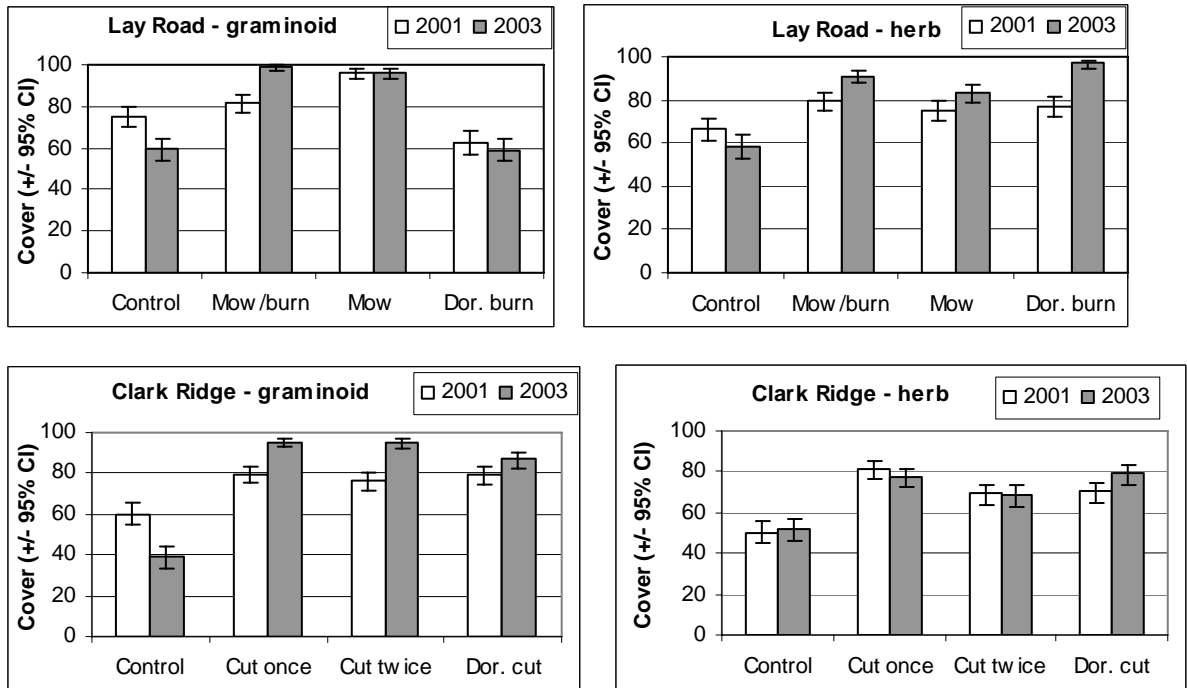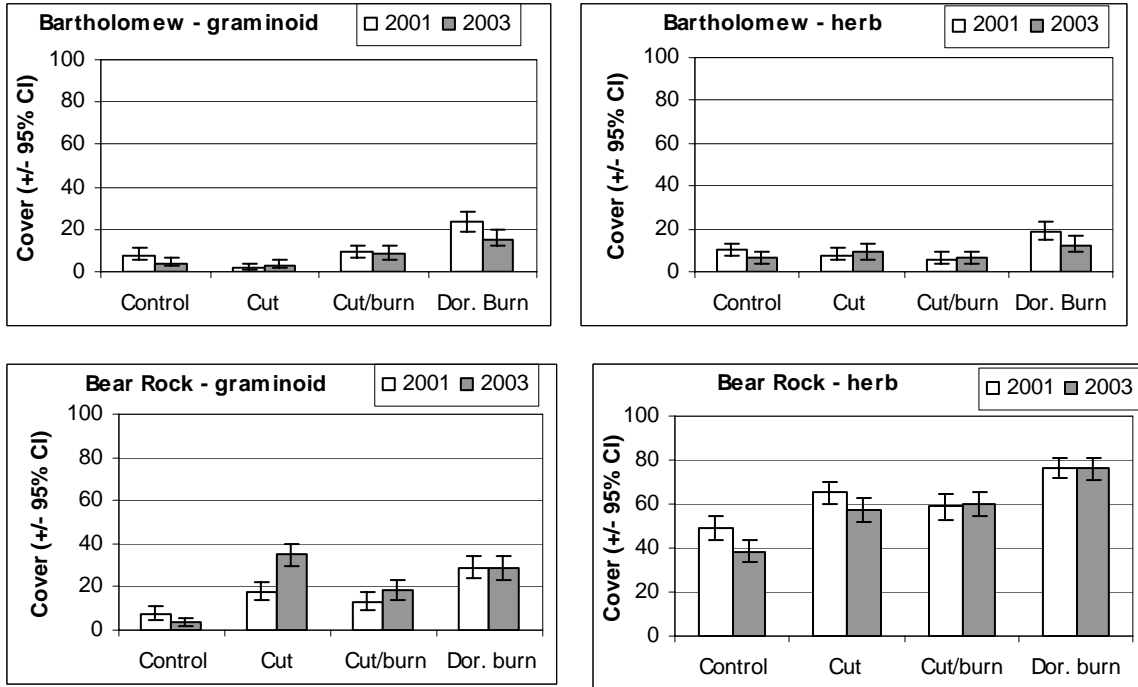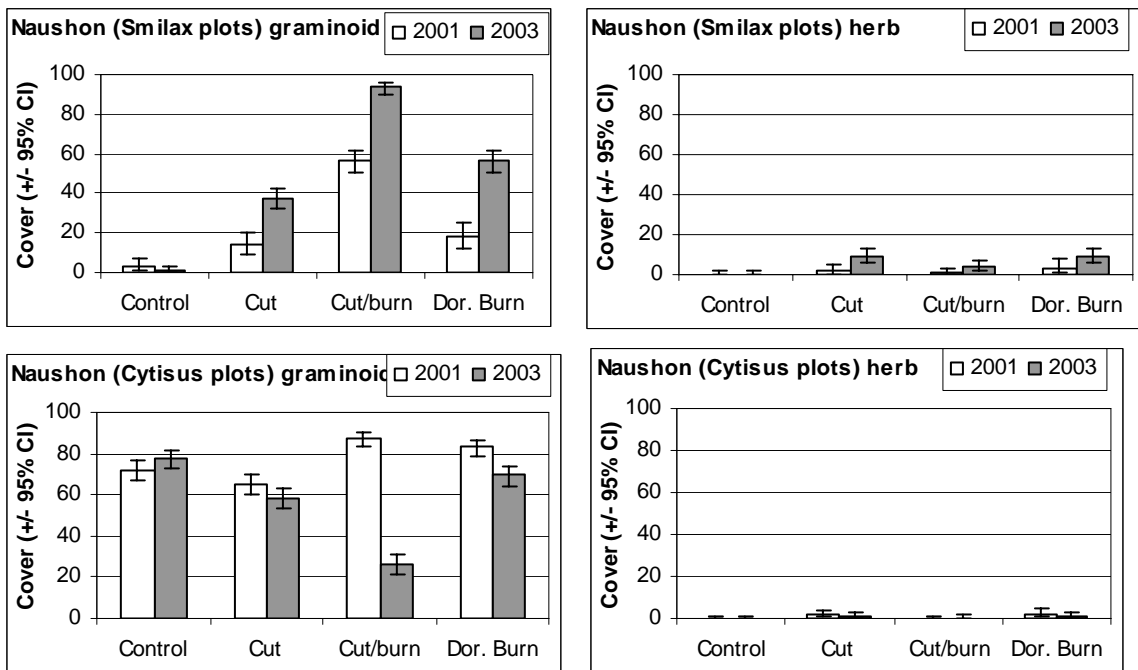

Figure 6-4. Graminoid and herb cover (and 95% confidence intervals) before (2001) and after (2003) treatments to control *Smilax rotundifolia and Cytisus scoparius* on Naushon Island.

The treatments applied during this study, whether cut or burn, in the growing or dormant season, resulted in at least temporary decreases in cover and height (see Chapter 5) of the invasive shrubs. Although the shrub species persisted at the sites by sprouting, the temporary reduction of their cover resulted in varied responses by other plant species. Graminoid and herbaceous species, formerly shaded by the taller, dominant shrubs, generally increased in cover or remained the same. Other shrub species similarly decreased in cover, as they were subject to the same treatments in most plots as the targeted invasive. Species diversity and cover generally decrease with increasing invasive shrub cover (Woods 1993, Hutchinson & Vankat 1997, Collier *et al.* 2002, Frappier *et al.* 2003), a relationship that I also observed, although I examined recovery of species rather than loss. Cover of graminoids and herbs did not vary with the season or type (cut vs. burn) of treatment, except with the growing season fires at Lay Road and the *Cytisus* plots on Naushon. Graminoid cover significantly increased following summer burning at Lay Road, but decreased in the *Cytisus* burn plots. No relationship with burning was found for the other sites, but those sites were also not successfully burned during the growing season. Individual species within these two broad growth forms may have been influenced differently by the variety of treatments, but this was not evaluated in this study. The change in dominance from the invasive shrub to non-woody species is only temporary, while the shrub sprouts are not tall enough to shade the other species.

The strength of the relationship between the cover of invasive shrubs and that of other species depends on the habitats studied. The cover of graminoids and herbs at the Montezuma NWR fields varied little as a result of treatment. These fields have been managed with periodic mowing and burning for at least 15 years (Mitchell 2000). Many of the herbs and graminoids that occur in these fields are perennials which have persisted beneath the dominant shrubs.

Graminoid and herb cover at the Berkshire sites did not vary, except for an increase in graminoids in the Bear Rock Stream cut plot. Understory species cover at the Bartholomew site dominated by *Berberis* did not change following treatments. Silander and Klepeis (1999) report similar results for a *Berberis*-dominated site in Connecticut. This lack of recovery following *Berberis* removal may be due to limited light reaching the understory, poor seed dispersal and/or germination, or to underlying changes in soil nitrogen (Kourtev *et al.* 1999). At Naushon *Cytisus* plots treated with a burn (in either the growing or dormant season) exhibited significantly decreased graminoid cover, whereas all treatments in *Smilax* plots had increased graminoid cover. Herb cover in all Naushon plots was generally <5% before treatments and did not significantly change after treatments, although it tended to increase in the *Smilax* plots. Both *Cytisus* and *Smilax* form dense thickets with deep litter and duff layers which exclude many native grass and herb species. These native species may be slow to establish from seed once the invasive is gone, especially if litter and duff layers are not removed.

Changes in species richness were not significantly related to cover of the invasive species following treatments. Richness remained the same (or varied only slightly) in the Berkshire and Naushon Island plots. This stability may be the result of slow dispersal of new species, unsuitable conditions for seedling germination and establishment, and underlying changes in soil chemistry due to the invasives (Kourtev *et al.* 1999, Gardescu & Marks 2004). Alternatively, a complement of species may have occurred under the invasive shrubs prior to treatment, although their abundance (cover and density) was minimal and therefore their presence could have been overlooked. A similar situation was reported by Richburg *et al.* (2001) for plots with and without the invasive grass *Phragmites,* where richness was similar, but the cover and density of species under the grass cover was reduced. The increase in richness for the Montezuma NWR plots (up to 78% more species following treatment) may represent species which were not identified beneath the dense shrub canopy prior to treatment. Many grass and herb species flowered following removal of *Cornus* allowing them to be identified and contribute to the observed increase in richness. Five of the nine graminoids and as many as ten herbs where not identified to species until after treatments. Species richness at this site is likely related to the repeated disturbances (mowing, prescribed fire) that have occurred over the past several decades. Shade-intolerant species may be able to persist as weak, vegetatively reproducing individuals or in the soil seedbank until shrub cover is removed. Without periodic control of the shrubs, these species may eventually be eliminated from the site.

Invasive plant species alter natural communities by competing with other species for resources, changing habitat structure and composition, and influencing ecosystem processes. As the shrub species included in this study invaded the old field, grassland, and forest understory habitats of the study sites, the structure and diversity of the communities presumably changed as has been reported from other sites. Reduction, at least temporarily, of invasive shrub cover altered the vigor of other species. Without further treatments shrubs will again dominate these areas as sprouts grow rapidly.

Removal of invasive plants is important to restoring diversity and structure of natural communities, although attempts to eradicate a well-established invasive should proceed with caution as removal may cause unforeseen changes in plant species composition and ecosystem function (Westman 1990, Hobbs & Humphries 1995). In some cases, complete restoration may not be possible due to large changes in soils or other factors caused by the establishment of the invasive or previous land use. Consideration must also be given to what will happen following removal. Will native species reestablish at the site through natural dispersal or will plantings be required? Is the site likely to be re-invaded by the species removed or other invasive species, and if so how can that be prevented? Although *Cytisus* was killed with the treatments in this study, it readily germinated from seeds present in the soil and dispersed from nearby individuals. Prevention of reestablishment of this species, like that of many others, requires follow-up treatments to eliminate seedlings (Randall & Marinelli 1996, Frappier *et al.* 2004, Rice 2004). In order to preserve biodiversity, natural areas managers must

consider these questions when making difficult decisions on how and when to control

problem invasive plants.

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CHAPTER 7

CONCLUSION

In the northeastern United States, invasive woody plants occur in disturbed areas and are spreading into natural areas. These shrubs, vines, and trees affect other species directly through competition and indirectly by altering habitats and ecosystem processes. Agencies and organizations concerned with the preservation of biodiversity are studying these species to learn more about their biology, their effects on native species and natural processes, and ways to control or eliminate them. Appropriate control methods depend on the physiology of the target species, size of infestation, habitat type, and local or regional regulations. Methods include hand-pulling, cutting, burning, herbicide, biocontrols, or a combination of these. Many woody invasive species present particular problems for control efforts as they readily sprout when injured. Cutting or burning these species can temporarily reduce their above-ground stature, but unless the roots are killed the plants will persist at the site. Treatments when root reserves are high (i.e. during the dormant season) can actually stimulate clones to expand and/or plants to flower, fruit and spread additional seeds.

Carbohydrates stored in the roots of woody plants support growth of sprouts following removal of stems or leaves and generally follow an annual cycle of depletion and replenishment. This study documents the impacts that mechanical and prescribed fire treatments, timed to key points in the carbohydrate reserve cycle, have on seven

woody invasive species. To more completely understand how the treatments affect

shrubs, I evaluated changes in both above- and below-ground structures (i.e. sprout

growth and carbohydrate reserves, respectively). Because treatments were applied to the

target invasives *in situ*, I also evaluated the impact of shrub decline on plant community

composition.

The concentration of root carbohydrate reserves (TNC) varied among species,

sites, month of treatment application, and climatic conditions. When left untreated,

Cornus, *Rhamnus*, *Rosa*, *Berberis*, *Lonicera*, and *Smilax* depleted their reserves in the

spring and replenished them during the growing season, as expected. Spring minima for

reserves generally occurred by late May (although *Lonicera* was much earlier) with

recovery generally requiring 4 to 5.5 months, except for *Berberis* which replenished

reserves in a month. Overall, without treatments, *Smilax* roots had the lowest TNC and

Rosa the highest. *Cornus* and *Rhamnus* TNC varied more than other species with respect

to minima and maxima. Dry conditions result in decreased photosynthesis, so variation

in TNC between years in untreated plots might be at least partially attributable to soil

drought.

Treatments applied included cutting and/or burning in either the dormant or

growing seasons. Dormant-season treatments (whether cutting or prescribed fire) top-

killed shrubs which then sprouted and replenished below-ground carbohydrate reserves

(except for *Cytisus*), often within just a few months of treatment. Alternatively, growing-

season treatments resulted in slower recovery of reserves for *Cornus*, *Rhamnus*, *Rosa*,

Berberis, *Lonicera*, and *Smilax* as carbohydrate reserves were additionally depleted before they were replenished from spring minimums. Multiple treatments during a single growing season kept TNC reserves low during the season of treatment and into the next growing season. No treatments were applied during the third growing season and TNC replenished to pretreatment levels by that autumn in all species studied. Invasive shrub species, with their ability to sprout and rapidly replenish TNC reserves, will again dominate these sites without further control efforts.

Heights and mass of shrub sprouts were generally positively correlated with the concentration of underground root reserves. Prior to treatment, plants treated in the dormant season had near-maximum TNC reserves, whereas those treated in the growing-season had near-minimum TNC. During the three-year study, sprout growth following growing-season treatments did not equal that following dormant-season treatments, even when given more time to grow following treatment. Dormant-season treatments do little more than reduce the height of shrubs, and often increase stem density. Growing-season-treated plants, although still able to sprout, produce less sprout mass due to decreased carbohydrate reserves. The more frequently growing-season treatments were applied, the less sprout biomass was produced following each treatment. For *Cornus*, *Rhamnus*, *Berberis*, and *Smilax,* the difference in sprout biomass produced by plants receiving two vs. three treatments was notable, whereas that between three and four treatments was less. This may reflect a loss of root biomass as well as a decrease in TNC concentrations.

Although all the invasive shrubs persisted at the sites by sprouting (except *Cytisus* which only minimally sprouted but produced abundant seedlings), reductions in cover allowed other species, particularly graminoid and herbaceous plants, to flourish. Other studies have reported that increased cover of invasive shrubs leads to decreased diversity and cover of other species (Woods 1993, Hutchinson & Vankat 1997, Collier *et al*. 2002, Frappier *et al*. 2003). The reverse was true following treatments in this study, indicating that the trend of losing species due to an invader can be reversed with its removal in some situations. The length of the invasion and the species involved influence the success of restoration. The cover of graminoids and herbs did not vary consistently with season or type (cut or burn) of treatment beyond the influence that the treatments had on cover of the invasive shrub. Changes in species richness were not significantly related to cover of the invasive species following treatments, perhaps due to this study's short time-frame.

Controlling woody invasive species is difficult due to their ability to sprout following most treatments. Although above-ground biomass is reduced (resulting in decreased cover), without further treatment the production of vigorous sprouts will lead to recovery of pre-treatment cover. Multiple growing-season treatments of the seven target species in this study reduced the vigor of sprout growth, although none of the species was eliminated. Additional growing-season treatments beyond those applied in this study could further stress existing root systems resulting in decreased sprout vigor, death of additional roots, and increased susceptibility to disease or competition. Therefore even if these species are not eliminated, their impacts on other species can be reduced by decreasing the invasive shrubs' vigor.

To preserve biodiversity, natural areas managers are faced with difficult decisions on how and when to control or eliminate problem invasive plants. More research is needed to provide this information. Several key questions should be pursued. Additional research is needed to determine the number of treatments necessary to effectively control the seven woody invasives included in this study as well as other problem species, with the understanding that site factors, species physiology, and age of the population can influence TNC reserves. Combining treatment types may increase their effectiveness and speed of control. Cutting treatments may be necessary to supply enough fuel to carry a growing-season fire. In other cases, a prescribed fire can increase visibility of large hazards (e.g. rocks) before mechanical treatments are applied. Cutting and burning treatments are effective at reducing overall biomass and height of invasive shrubs, which can reduce the amount of herbicide necessary to control a population. Although herbicides can be applied successfully, alternatives such as repeated cutting may be necessary or preferred depending not only on the biology of the species or habitat but also on socioeconomic factors such as regulations or acceptance of herbicide use.

Invasive species have impacted native species and ecosystems, and their removal could have positive or negative effects. Attempts to control a population of an invasive plant should follow not only how the target species is reacting, but also how the control is affecting other species. Desirable species could decline if they are also sensitive to the treatments being applied. The control methods being used can be altered to be more species specific in such cases. Removal of one invasive species may also allow for

invasion by another that is less desirable and harder to control. Elimination of shade-intolerant exotic species from old fields by allowing succession to occur is now resulting in invasion by shade-tolerant non-native species in New Jersey (Meiners *et al*. 2002). In some instances invasives can be successfully removed from a site, but in the majority of instances we can only hope to decrease their presence enough to reduce the negative impacts on natural communities and other species. This will require continued management and careful vigilance for new invasives in important natural areas.

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