POTENTIAL ECOLOGICAL EFFECTS OF SUDDEN OAK DEATH ON MESIC OAK FORESTS IN THE SOUTHERN APPALACHIANS

by

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(Under the Direction of Ronald L. Hendrick, Jr)

ABSTRACT

The causal agent of sudden oak death (SOD), *Phytophthora ramorum*, is expected to eventually invade forests in the southern Appalachians. Dominant overstory and understory species, *Quercus rubra* L. and *Rhododendron maximum* L., respectively, are susceptible to the pathogen and may be affected by SOD. The objective was to quantify the effects of simulated SOD on under two possible scenarios: (1) a moderate severity outbreak of SOD with high mortality of Q. *rubra* only, and (2) a high severity scenario in which the *R. maximum* understory would be severely impacted in addition to *Q. rubra*. Results show subtle changes in herbaceous layer vegetation and seedling establishment in scenario 1 and pronounced changes in scenario 2; changes in litterfall under both scenarios; and pronounced changes in soil respiration in scenario 2.

INDEX WORDS: disease, disturbance, ecology, forest, pathogen, *Phytophthora ramorum*, *Quercus rubra*, *Rhododendron maximum*, soil, sudden oak death

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DEDICATION

To my husband, Jason Thomas Watkins, for his support and encouragement on my path to becoming a botanist and ecologist.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

POTENTIAL SUDDEN OAK DEATH IN THE SOUTHERN APPALACHIANS

Phytophthora ramorum (Werres, De Cock and Man in't Veld), an oomycete fungus in the Kingdom Stramenopila, spreads by spores, affects only aboveground plant parts, and infects a broad range of species including red oaks (*Quercus,* section *Lobatae*) and woody species in the family Ericaceae. It was first described as a pathogen on *Rhododendron* spp. in Germany (Werres et al. 2001), however recent research based on ecological niche modeling places the origin of *P. ramorum* as eastern Asia (Kluza et al. 2007). Foliar and stem infection of nursery and garden specimens of *Rhododendron catawbiense Michx.*, a species native to the Southern Appalachians, has led to mortality in Europe (Werres et al. 2001). Sudden oak death (SOD), of which initial outbreaks in the mixed hardwood forests of California caused “sudden” unexplained mortality of oaks (*Quercus* spp.) and tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.), is now identified as an infection by *P. ramorum* from central California to southern Oregon (Werres et al. 2001, Rizzo et al. 2002a, Rizzo et al. 2002b, Goheen et al. 2002, Rizzo and Garbelotto 2003, Garbelotto and Rizzo 2005). It reached epidemic levels in central California and killed tens of thousands of trees (Rizzo and Garbelotto 2003, and Garbelotto and Rizzo 2005). A broad range of plant species, from ferns to redwoods, have tested positive as carriers of *P. ramorum* (Garbelotto and Rizzo 2005). Non-lethal infection of California bay laurel

(*Umbellularia californica*), a dominant understory shrub, has created a persistent source of innoculum in soil and water (Maloney et al. 2005, Davidson et al. 2005, Fichtner et al. 2007).

Ecological and climate models suggest that climate and species composition make southeastern U.S. forests highly susceptible to infection (Kluza et al. 2007, Venette and Cohen 2006). Shipments of azaleas (*Rhododendron* spp.) and camellias (*Camellia* spp.) from California nurseries to the southeastern U.S. have contained *P. ramorum* and it is highly likely that SOD will eventually spread to southeastern U.S. forests (Stokstad 2004). Numerous herbaceous and woody species, particularly red oaks and Ericaceous species, are susceptible to infection with varying degrees of expected disease effects and mortality.

Of particular interest in the southern Appalachians is the likely susceptibility of oaks, particularly northern red oak (*Quercus rubra*), and rosebay rhododendron (*Rhododendron maximum*, a close relative of *R. catawbiense*). Red oak lumber is valued for furniture and flooring and *Q. rubra* acorns are a major food source for wildlife, including white tailed deer, wild turkey, and black bears (de Steiguer et al. 1989, McShea and Healy 2002). *Q. rubra* is a dominant overstory species in the southern Appalachians, but could lose dominance in the forest canopy if affected by an outbreak of sudden oak death (Davidson et al. 2003). *R. maximum* is a dominant shrub that plays a significant role in regulating forest dynamics by restricting regeneration and understory development via its dense shade and recalcitrant litter (Monk et. al 1985).

Early pathogenicity testing indicated that *Q. rubra* and *R. maximum* are susceptible in vitro to *P. ramorum*, while a recent greenhouse study on seedlings suggests *Q. prinus* and Q. *alba* may be more susceptible than *Q. rubra* (Werres et al. 2001, Tooley et al. 2004, Tooley and Kyde 2007). Mortality of *Rhododendron* spp. and infection of *Q. rubra* has been reported from

Europe and both *Q. rubra* and *R. maximum* in southern Appalachian forests are expected to experience some degree of mortality due to SOD (Werres et al. 2001 and Brasier et al. 2004). Horticultural specimen *Q. rubra* trees in Europe developed canker infection at the trunk, similar to oaks and tanoaks in California and Oregon (Brasier et al. 2004). SOD is expected to progress in *Q. rubra* as in other oaks and tanoaks, eventually girdling the tree and causing mortality. *R. maximum* is expected to develop a foliar infection, as in rhododendrons in Europe, with effects anywhere from a persistent non-lethal infection, as occurs in California bay laurel, to a fatal disease, as with European rhododendrons (Maloney et al. 2005, Davidson et al. 2005, Fichtner et al. 2007, Werres et al. 2001).

MESIC OAK FORESTS IN THE SOUTHERN APPALACHIANS

Disturbance is common in southern Appalachian forests and historically includes wind, logging, fire, and disease (Douglass and Hoover 1988). Disturbance disrupts the trajectory of a forest towards a climax community, creating conditions for secondary succession and seedling recruitment (Chapin et al. 2002b). Severe disturbance can alter ecosystem production, decomposition, and nutrient cycling by creating a pulse of litter from destroyed plants; alter plant community composition, which in turn determines litter quantity and quality; create canopy gaps with concomitant changes in microclimate; and directly displace or disturb soil (Chapin et al. 2002a).

Windthrow disturbance, which creates pit and mound topography that affects seedling recruitment, is common in forests of the eastern U.S. and is well documented at the Coweeta Hydrologic Laboratory (Clinton and Baker 2000). Early European colonists converted low areas into agricultural fields and the forest was heavily logged prior to acquisition by the USDA Forest

Service in the early 1900s (Douglass and Hoover 1988). As the human population in the region continues to grow, urbanization is increasingly relevant to forest management. One consequence of urbanization and management for human values is active fire suppression, which in combination with gaps in the forest due to the loss of chestnut, has allowed *R. maximum* to become a dominant species (Day et al. 1988).

Lightning caused natural fires and Native Americans used fire to manipulate habitat for game and to herd animals for hunting (Douglass and Hoover 1988, Delcourt and Delcourt 1997). The practice of burning woodlands was continued by early European colonists to provide forage for grazing livestock (Douglass and Hoover 1988). Current management practices include the use of prescribed fire to stimulate herbaceous forage, promote fire tolerant oaks, and suppress fire intolerant Ericaceous shrubs (*R. maximum* and mountain laurel, *Kalmia latifolia*) and shade tolerant hardwood species (i.e. red maple, *Acer rubrum*) (Elliot et al. 1999).

Introduced forest diseases have been common in the southern Appalachians since European colonization. Present day southern Appalachian forests have been shaped by the legacy of chestnut blight caused by the canker pathogen *Cryphonectria parasitica* (Day et al. 1988, Elliot and Swank 2008). In 1934, American chestnut (*Castanea dentata*) made up 41% of the basal area in one watershed at Coweeta Hydrologic Laboratory in western North Carolina, yet by 1953, after infection with *C. parasitica*, *C. dentata* was reduced to less than one percent of the basal area of the same watershed (Nelson 1955). *C. dentata* persists as a minor species in the shrub layer of the forest by sprouting suckers from roots which are not infected by *C. parasitica* (Day et al. 1988, Ellison et al. 2005). Forests once dominated by *C. dentata* are now composed primarily of oaks and red maple (*Acer rubrum*), while rosebay rhododendron (*Rhododendron maximum*) dominates in the understory (Day et al. 1988, Elliot and Swank 2008). Gaps created by the loss of *C. dentata* were filled in by: 1) expansion of adjacent surviving trees, often chestnut oak (*Quercus prinus*) and northern red oak (*Quercus rubra*); 2) growth of existing seedlings in the regeneration layer; and (3) newly established seedlings that germinated from wind-dispersed seeds of red maple (*Acer rubrum*), black birch (*Betula lenta*), and yellow poplar (*Liriodendron tulipifera*) (Nelson 1955, Day et al. 1988, Elliot and Swank 2008).

The composition of southern Appalachian forests is threatened by two exotic insect pests of note, gypsy moth (*Lymantria dispar*) and hemlock wooly adelgid (*Adelges tsugae* Annand, HWA). While gypsy moths have not yet reached the southern Appalachians, due to the dominance of oak species southern Appalachian forests have been identified as highly susceptible to gypsy moth infestation (Liebhold 2008.) Gypsy moth preferentially feeds on oak leaves and causes widespread defoliation during periodic outbreaks (Elkinton et al. 2002). In northeastern forests, oak mortality is rare and defoliation by gypsy moths has not eliminated oaks, but has reduced their canopy dominance and allowed co-occurring species, such as *A. rubrum*, to increase in size (Elkinton et al. 2002, Lovett et al. 2006). HWA is presently spreading rapidly in the southern Appalachians and threatens to eliminate Eastern hemlock (*Tsuga canadensis*), opening gaps for further expansion of *R. maximum*, growth increases of existing hardwoods (oaks, *A. rubrum*, and *B. lenta*), and recruitment of early successional species (*A. rubrum*, *B. lenta*, *L. tulipifera*) and leading to changes in microclimate, litter quality, and soil nutrients (Brown 2004, Ellison et al. 2005, Martin and Skolochenko 2007, Nuckolls 2007).

SOD will likely result in non-random species loss, potentially changing the structure of the plant community and affecting community and ecosystem processes. The study area, located at Coweeta Hydrologic Laboratory in western North Carolina, is characterized by a mesic oak (-

chestnut) forest with an oak overstory and either a rich herbaceous layer or patches of thick *R. maximum* in the understory which suppress herbaceous species. Openings in the forest canopy would allow recruitment to occur, except in areas with dense *R. maximum* cover. In previous studies of canopy gap effects in the southern Appalachians, red maple seedlings dominated recruitment under such conditions (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000). Wildlife, dependent on oak acorns for food in winter, would be negatively affected by a change in the dominant overstory from oak to maple.

R. maximum inhibits recruitment of tree seedlings by restricting light and nutrient availability on the forest floor beneath it (Nilsen et al. 2001, Beier et al. 2005, Wurzberger and Hendrick 2007). A recent study of suppression of oak seedlings shaded by *R. maximum* found that photosynthesis was reduced and seedlings were limited by carbohydrate availability, which in turn limited their capacity to produce defensive compounds, making them more susceptible to herbivory (Beier et al. 2005). Even after removal of overstory canopy, thickets of *R. maximum* inhibit the growth of woody seedlings (Clinton et al. 1994, Beckage et al. 2000). In the event of an outbreak of SOD, *R. maximum* thickets could be defoliated and regrowth would be moderated by further infection by *P. ramorum*. The loss of the dense *R. maximum* cover could significantly increase recruitment of woody species, such as *A. rubrum*, (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000).

Changes in plant community structure and diversity due to disturbance have the potential to affect ecosystem production, decomposition, and nutrient cycling, which, in turn, determine plant species composition (Chapin et al. 2002b, Wardle 2002.). The severity of SOD impact in the forest will depend on the timeframe of infection and progression of the disease; the actual mortality of trees and shrubs, and the resistance and resilience of the plant community. Based on previous studies, we expect that loss of *Q. rubra* and *R. maximum* would result in an initial pulse of leaf and woody litter aboveground and an increase in belowground root litter via root death (Schroeer et al. 1999, Nuckolls et al. In Press). After the initial pulse in litter, plant productivity would temporarily decrease due to lack of vegetation in gaps created above- and belowground. In the case of loss of *Q. rubra* alone, productivity would recover relatively quickly by existing vegetation filling in gaps; however, if both *Q. rubra* and *R. maximum* are lost, productivity would take longer to recover due to the extensive loss of vegetation (Schroeer et al. 1999). Eventually, other hardwood species such as *A. rubrum* would replace *R. maximum* and *Q. rubra* lost to SOD (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000). A severe outbreak of SOD would lead to the replacement of recalcitrant, high lignin: nitrogen (N) *R. maximum* and *Q. rubra* litter by other litter, potentially increasing soil pH, N availability, and labile soil carbon (C), leading to an increased rate of decomposition. Over the long-term, the shift in litter quality (i.e. lower C:N, higher quality) would lead to a change in the soil microbial community, which would transform from a recalcitrant system dominated by mutualistic mycorrhizal fungi to a more fertile bacteria dominated assemblage (Wardle 2002).

Disturbance may directly disrupt soil or indirectly alter litterfall quality and quantity, and the effects of disturbance on soil organisms can be inferred by observing changes in soil respiration (Chapin et al 2002b, Vose and Bolstad 2007). Soil respiration reflects the combined biological activity of autotrophic and heterotrophic soil organisms and is measured as the rate of CO_2 evolved from the soil, often referred to as soil CO_2 efflux (Coleman et al. 2004). About half of soil respiration is contributed by decomposer organisms processing detritus and the remaining half is from living plant roots, their mycorrhizal fungi and other root-associated microbes, with soil fauna and free living microbes contributing a nominal amount (Kuzyakov 2006, Högberg and Read 2006). Disturbance can alter soil respiration via changes in soil temperature and moisture, which are considered the most influential factors on soil CO_2 efflux. (Vose et al 1995, Bolstad and Vose 2005). Logging in southern Appalachian forests temporarily decreases soil respiration, which recovers over time if the forest regrows, but if forests are converted to pasture, soil respiration is set at a new, lower rate (Bolstad and Vose 2005, Vose and Bolstad 2007). Litter exclusion has been shown to reduce soil respiration in the southern Appalachians and girdling of *Tsuja canadensis* reduced soil CO_2 efflux in the first two years after treatment (Reynolds and Hunter 2001, Nuckolls et al. In Press). SOD is expected to lower soil respiration by altering litterfall and soil temperature and moisture, and, depending on the severity of its effects, could reset the forest to a new, lower, rate of average soil respiration.

PURPOSE AND DESCRIPTION OF THIS STUDY

While there have been several epidemiological studies of the spread of *P. ramorum*, ecological studies of its effect on community and ecosystem dynamics are lacking. Land managers will be faced with the challenge of adjusting to a new species composition in the face of ecological changes arising from SOD. Short-term impacts (e.g. oak cankers and *R. maximum* foliar infection) of the disease will be apparent within a few years of infection, while longer-term effects will arise from the gradual mortality of individual trees and the successive establishment and growth of a new species mix. Data on community and ecosystem responses are needed to support appropriate management decisions.

The objective of this study was to quantify the short-term effects of simulated SOD under two possible scenarios. Under the first scenario, *Q. rubra* were girdled to simulate a moderate severity SOD outbreak with high mortality of red oaks only, which are considered highly susceptible to *P. ramorum*. The high-severity scenario treatment, with red oaks girdled and *R. maximum* cut and removed from the site, is intended to simulate the loss of both red oak and rhododendron, with the concomitant loss of aboveground biomass and litter input. In chapter 2, I address potential aboveground effects of SOD on herbaceous layer vegetation and seedling establishment. I present analyses of herbaceous layer species richness, community similarity, and percent cover and report woody seedling density, abundance, and species composition. In chapter 3, I address potential belowground effects of SOD and report differences in aboveground litterfall amount and composition along with analysis of soil temperature, moisture, and respiration. Finally, in Chapter 4, I combine current knowledge about southern Appalachian plant and soil ecology and SOD with conclusions from the plant and soil experiments to create a conceptual model of the potential effects of SOD in the Southern Appalachians.

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CHAPTER 2

POTENTIAL EFFECTS OF SUDDEN OAK DEATH ON PLANT COMMUNITY COMPOSITION OF A MESIC OAK FOREST IN THE SOUTHERN APPALACHIANS[1]

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[1] Watkins, M. H. M. and R. L. Hendrick. To be submitted to *Forest Ecology and Management.*

ABSTRACT

The causal agent of sudden oak death (SOD), *Phytophthora ramorum*, is expected to eventually invade forests in the southern Appalachians. Dominant overstory, *Quercus rubra* L., and understory, *Rhododendron maximum* L., species are susceptible to the pathogen and may be affected by SOD; loss of these dominant species could come at substantial ecological and economic cost. The objective of this study was to quantify the effects of simulated SOD on herbaceous layer vegetation and seedling establishment under two possible scenarios: (1) a moderate severity outbreak of SOD with high mortality of northern red oak, *Q. rubra* only, and (2) a high severity scenario in which the *R. maximum* understory would be severely impacted in addition to *Q. rubra*. Results from the first two years post-treatment demonstrate subtle changes in herbaceous layer vegetation and seedling establishment two years after treatment in the Girdle Only treatment and more pronounced changes in the Girdle + Removal treatment. Woody species richness and seedling density increased in the Girdle + Removal treatment. Summer estimates of similarity indicate that the plant community in southern Appalachian forests may change with either scenario of SOD. Chi-square analysis indicates that woody species composition differed among treatments under both scenarios, however, changes in fall may not be valid due to small sample size. We expect that in the long-term, species richness, percent cover, and woody seedling density will decrease, as red maple (*Acer rubrum*) successfully colonizes and persists in gaps created by loss of *R. maximum* and *Q. rubra*. Effects on additional species identified as susceptible to *P. ramorum* are uncertain. Land managers will be faced with the challenge of adjusting to a new species composition in the face of ecological changes arising from SOD.

INTRODUCTION

Disturbance is common in southern Appalachian forests and historically includes wind, logging, fire, and disease (Douglass and Hoover 1988). Present day southern Appalachian forests have been shaped by the legacy of chestnut blight caused by the canker pathogen *Cryphonectria parasitica* (Day et al. 1988, Elliot and Swank 2008). In 1934, American chestnut (*Castanea dentata*) made up 41% of the basal area in one watershed at Coweeta Hydrologic Laboratory in western North Carolina, yet by 1953, after infection with *C. parasitica*, *C. dentata* was reduced to less than one percent of the basal area of the same watershed (Nelson 1955). Forests once dominated by *C. dentata* are now composed primarily of oaks and red maple (*Acer rubrum*), while rosebay rhododendron (*Rhododendron. maximum*) dominates in the understory (Day et al. 1988, Elliot and Swank 2008). Gaps created by the loss of *C. dentata* were filled in by: 1) expansion of adjacent surviving trees, often chestnut oak (*Quercus prinus*) and northern red oak (*Quercus rubra*); 2) growth of existing seedlings in the regeneration layer; and (3) newly established seedlings that germinated from wind-dispersed seeds of red maple (*Acer rubrum*), black birch (*Betula lenta*), and yellow poplar (*Liriodendron tulipifera*) (Nelson 1955, Day et al. 1988, Elliot & Swank 2008)

Southern Appalachian forests now face a new threat: sudden oak death (SOD), a disease predicted to cause the loss of ecologically, economically, and aesthetically valuable species and potentially change the structure of the plant community even more dramatically than chestnut blight. Ecological and climate models suggest that climate and species composition make southeastern U.S. forests at high risk for SOD (Kluza et al. 2007, Venette and Cohen 2006). Numerous herbaceous and woody species are susceptible to infection by *Phytophthora ramorum* (Werres, De Cock and Man in't Veld), the fungus that causes SOD, with varying degrees of expected disease effects and mortality. Of particular interest in the southern Appalachians is the likely susceptibility of oaks, particularly northern red oak (*Quercus rubra*), and rosebay rhododendron (*Rhododendron maximum* L.). Early pathogenicity testing indicated that *Q. rubra* and *R. maximum* are susceptible in vitro to *P. ramorum*, (Werres et al. 2001, Tooley et al. 2004). Shipments of azaleas (*Rhododendron* spp.) and camellias (*Camellia* spp.) from California nurseries to the southeastern U.S. have contained *P. ramorum* and it is highly likely that SOD will eventually spread to southeastern U.S. forests (Stokstad 2004).

P. ramorum, an oomycete fungus in the Kingdom Stramenopila, spreads by spores, affects only aboveground plant parts, and infects a broad range of species including red oaks (*Quercus*,section *Lobatae*) and woody species in the family Ericaceae. It was first described as a pathogen on *Rhododendron* spp. in Germany (Werres et al. 2001), however recent research based on ecological niche modeling places the origin of *P. ramorum* as eastern Asia (Kluza et al. 2007). Both *Q. rubra* and *R. maximum* are expected to experience some degree of mortality due to SOD based on reports of disease in Europe (Werres et al. 2001 and Brasier et al. 2004). Foliar and stem infection of nursery and garden specimens of *Rhododendron catawbiense* Michx. (Catawba rhododendron, a southern Appalachian native and close relative of *R. maximum*) has led to mortality in Europe (Werres et al. 2001). Horticultural specimen *Q. rubra* trees in Europe developed canker infection at the trunk and SOD progressed as in other oaks and tanoaks, eventually girdling the tree and causing mortality (Brasier et al. 2004). *R. maximum* is expected to develop a foliar infection, as have rhododendrons in Europe, with effects anywhere from a persistent non-lethal infection, as occurs in California bay laurel (*Umbellularia californica*), to a fatal disease, as with European rhododendrons (Maloney et al. 2005, Davidson et al. 2005, Fichtner et al. 2007, Werres et al. 2001).

R. maximum is a dominant shrub that plays a significant role in regulating forest dynamics by restricting forest regeneration and understory development. Stands of *R. maximum* cast dense shade and have recalcitrant litter (Monk et. al 1985). *R. maximum* inhibits recruitment of tree seedlings by restricting light and nutrient availability on the forest floor beneath it (Nilsen et al. 2001, Yeakley et al. 2003, Beier et al. 2005, Wurzberger and Hendrick 2007). Even after removal of overstory canopy, thickets of *R. maximum* inhibit the growth of woody seedlings and loss of dense *R. maximum* cover due to SOD could significantly increase recruitment of woody species, such as *A. rubrum* (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000). Wildlife, dependent on oak acorns for food in winter, would be negatively affected by a change in the dominant overstory from oak to maple. Oak seedlings shaded by *R. maximum* have reduced photosynthesis and are limited by carbohydrate availability, which in turn limits their capacity to produce defensive compounds, making them more susceptible to herbivory (Beier et al. 2005). Nitrogen concentrations in the soil and in nearby streams increased significantly after hardwood loss due to windthrow and nitrogen concentrations in the soil tripled after *R. maximum* removal (Yeakley et al. 2003). It is unknown how a possible increase in nitrogen availability could affect woody regeneration in forests infected with SOD.

The objective of this study was to quantify the effects of simulated SOD on herbaceous layer vegetation and seedling establishment under two possible scenarios. Under the first scenario, *Q. rubra* were girdled to simulate a moderate severity SOD outbreak with high mortality of red oaks only. The high-severity scenario treatment, with red oaks girdled and *R. maximum* cut and removed from the site simulated the loss of both red oak and rhododendron, with the concomitant loss of aboveground biomass and litter input. We hypothesized that herbaceous layer species richness, percent cover, and woody seedling density would increase as suppressive effects of *R. maximum* decline and *Q. rubra* mortality progresses. We expected these effects to be most evident in the Girdle + Removal treatment plots and did not expect to see dramatic treatment effects in the Girdle Only because of gradual mortality and continued suppressive effects of *R. maximum*.

METHODS

Site Description

The study area, located at Coweeta Hydrologic Laboratory in the Nantahala Mountains of western North Carolina (35°02' N, 83°27' W), is characterized by a mesic oak (formerly oak-chestnut) forest with an oak overstory and either a rich herbaceous layer or patches of thick *R. maximum* in the understory which suppress herbaceous species (Day et al. 1988). Red oak lumber is valued for furniture and flooring and *Q. rubra* acorns are a major food source for wildlife, including white tailed deer, wild turkey, and black bears (de Steiguer et al. 1989, Kirkpatrick and Pekins 2002). *Q. rubra* and *R. maximum* could lose dominance in the forest canopy if affected by an outbreak of SOD (Davidson et al. 2003).

The research plots are located at an elevation of 1200 m in a mixed hardwood forest with a significant understory of *R. maximum* and a northerly aspect. Mean annual precipitation is approximately 1800 mm, and is generally distributed evenly throughout the year (USFS 2008). Total annual precipitation at the Coweeta Hydrologic Laboratory climate station was 1549.6 mm in 2006 and 1212.9 mm in 2007 (USFS 2008). Mean annual air temperature is approximately 13 °C and ranges from -18 °C to 24 °C (Swift et al., 1988). Mean annual air temperature at the Coweeta Hydrologic Laboratory climate station was 14.1°C in 2006 and 14.3°C in 2007 (USFS 2008). Soil characteristics are typical for highly weathered Ultisols, being relatively high in organic matter and moderately acidic with both low cation exchange capacity and low percent base saturation (Swank and Crossley 1988).

Experimental Design

During winter 2004-2005, nine experimental plots (25 m x 25 m) were established in stands containing at least 15% *Q. rubra* basal area and with *R. maximum* patches covering at least 15% of the plot area. Eight plots are located around a central large *Q. rubra* tree, and one plot is located around a central large *Nyssa sylvatica* surrounded by three smaller *Q. rubra* trees. Plots were matched based on similarity of overstory composition and treatments randomly assigned in a complete block design. In each of three blocks, one plot was assigned to each of three treatments described below in Treatment Application.

Overstory and Understory

The pretreatment vegetation survey occurred in summer 2005 (Table 1). On each plot, all trees greater than 10 cm diameter at breast height (DBH = 1.37 m) were identified to species, tagged, and measured. All shrubs greater than 1 cm DBH were identified to species and recorded by size class. Basal area and density were calculated for trees and shrubs on each plot.

In fall 2005, percent canopy cover was estimated using a spherical densiometer (Table 1). Measurements were taken at 18 locations across each plot: 9 points along transects (3 points on 3 transects at roughly 10 m intervals, beginning at 5 m into the plot and running roughly along the contour parallel to the top and bottom) and at 9 sampling points established for the belowground portion of this study (see Chapter 3). On one plot a transect point overlapped with one of the sampling points, so that plot had only 17 locations. Percent canopy cover was estimated at each location as the average of measurements taken in four cardinal directions.

Treatment Application

In each block, one plot was randomly assigned to each of the three treatments: (1) control, (2) *Q. rubra* girdled, and (3) both *Q. rubra* girdled and *R. maximum* cut and removed. The girdling of *Q. rubra* and removal of *R. maximum* was conducted in February 2006. (Table 1) Trees were girdled with a chainsaw by cutting through the cambium of *Q. rubra* at the base of the tree. *R. maximum* trunks were cut at the ground level on most plots, To simulate a later stage of SOD, when *R. maximum* litter would no longer be contributed and seedlings would not be shaded, cut *R. maximum* limbs and trunks were manually removed from treatment 3 plots; however, several large pieces of *R. maximum* stems were limbed but left on one plot due to time constraints. The litter layer on *R. maximum* removal plots was disturbed as little as possible; however, some disturbance was unavoidable and was consistent across plots. *R. maximum* stumps resprouted during the growing season and emerging stems and leaves were periodically removed to simulate continued stress from belowground damage as well as reinfection by *P. ramorum*.

Herbaceous Layer Measurements

Four 4 m^2 subplots randomly located in each plot were surveyed for species richness, total percent cover, and woody seedling density in the herbaceous layer below breast height (1.37 m) (Table 1). *R. maximum* suckers sprouting from stumps were removed after annual fall surveys to simulate reinfection by *P. ramorum*. Pre-treatment total species richness and total percent cover were measured in summer (2005) and woody seedling richness and number of stems present were measured in fall (2005). Post-treatment herbaceous species richness was measured in the spring (2006 and 2007). Post-treatment total species richness and total percent cover were measured in the spring (2007) and summer (2006 and 2007). Post-treatment woody seedling richness and number of stems present were measured in the spring (2007), summer (2006 and 2007), and fall (2006 and 2007). Due to their abundance and time constraints, bear huckleberry (*Gaylussacia ursina)* stems were counted only during each fall survey.

Statistical Analysis

Statistical analyses were based on a randomized complete block design with three blocks in which one plot in each block was assigned to each of the three treatments: Control, Girdle Only, and Girdle + Removal. One way repeated measures analysis of variance (ANOVA) was calculated for all herbaceous layer measurements. Effects of time and time*treatment were calculated within plots and treatment effect was calculated between plots. Multiple comparisons were calculated with one way ANOVA. Differences among treatments in species composition of woody seedlings was evaluated using a chi-square test. The five most abundant species were represented individually while all other species were pooled into an “other” category to satisfy the test assumptions. Non-metric multidimensional scaling (NMS) ordination was used to compare woody seedling species composition across plots.

To qualitatively compare pre- and post-treatment community similarity, Jaccard’s index and the incidence-based Chao-Jaccard index were calculated for summer and fall presence-absence data using EstimateS 8.0.0 (Chao et al. 2005). The classic Jaccard's index is sensitive to sample size, particularly when numerous rare species are present but not encountered during surveying (Chao et al. 2005). The Chao-Jaccard index was designed to account for species missed in surveying by using replicated incidence (i.e. presence-absence) data in a probabilistic derivation of the classic Jaccard's index to improve the accuracy and interpretation of results (Chao et al. 2005). For summer and fall, the 2005 pre-treatment sample was compared to the 2006 post-treatment sample, and again with the 2007 post-treatment sample to assess the change in community similarity over time. ANOVA was calculated for the classic Jaccard index, but significance could not be determined for the Chao-Jaccard index, which, due to the nature of the derivation, is calculated as a single measurement for each sample. All tests were evaluated for significance at alpha = 0.05.

RESULTS

Overstory and Understory

Thirty four woody species were identified in the pre-treament survey (Appendix B). Total pre-treatment basal area of trees and shrubs was similar across treatments, ranging from 34.6 to 40.2 m^2 ha^{-1} (Table 2, Appendix B). *Q. rubra* basal area ranged from 9.6 to 13.3 m^2 ha^{-1} while *R. maximum* basal area was between 2.1 and 4.9 m^2 ha^{-1}. *Q. rubra* comprised an average of 30.3% of pretreatment basal area, followed by *A. rubrum* at 21.0%, *Q. prinus* at 17.2%, *R. maximum* at 8.4%, *Carya glabra* at 5.0%, and *Betula lenta* at 4.4%, together accounting for 86.3% of basal area (Appendix B). Pre-treatment stem density was greater in control than treatment plots, due to a single plot having a large number of small diameter stems (Table 2, Appendix B). Pre-treatment estimated canopy cover was similar across treatments and ranged from 83.4 % (sd = 8.7) in plots assigned the Girdle + Removal treatment to 87.4 % (sd = 9.5) in plots assigned the Girdle Only treatment and 86.1 % (sd = 9.4) in plots assigned to Control.

Herbaceous Layer Species Richness

Treatment differences in summer total richness were consistent across years, affected by treatment but not time*treatment interactions (Appendix D). Total richness ranged from 1.5 to 3.4 species m^{-2} and was consistently greater in Girdle + Removal treatment than Control or Girdle Only before and after treatment in summer (Fig. 2.1). Girdle + Removal treatment significantly increased total richness in summer 2006 and 2007 relative to Girdle Only treatment (Fig. 2.1). Treatment differences in fall woody species richness were consistent across years, affected by treatment but not time*treatment interactions (Appendix D). Girdle + Removal treatment fall woody species richness ranged from 0.8 to 1.5 species m^{-2} and was significantly greater than Girdle Only treatment in 2006 and 2007 (Fig. 2.2). Differences in spring herbaceous species richness were consistent across treatments, affected by time but not time*treatment interactions (Appendix D). Spring herbaceous species richness ranged from 0.7 to 1.5 species m^{-2} and was greater in 2007 than 2006 for all treatments (Fig. 2.3).

The classic Jaccard index was less for the Girdle Only and Girdle + Removal treatments in summer 2005-2007 than summer 2005-2006, indicating that both treatments are less similar to pretreatment (2005) in summer 2007 than summer 2006 (Fig. 2.4a). Control treatment samples were more similar to pretreatment (2005) in summer 2007 than summer 2006 (Fig. 2.4a). However, differences in the classic Jaccard index were not statistically significant. The incidence estimated Chao-Jaccard index was less for the Girdle Only and Girdle + Removal treatments in summer 2007 than summer 2006 (Fig. 2.4b). This indicates that both the Girdle Only and Girdle + Removal treatments were less similar to pretreatment in 2007 than 2006. Differences in the classic Jaccard index between treatments and years for fall dates were not significant and the incidence estimated Chao-Jaccard index does not indicate a change in similarity with pretreatment for fall 2006 versus fall 2007 (Fig. 2.5).

Percent Cover

Total herbaceous layer (<1.37 m in height) percent cover was greatest in control plots, lower in Girdle Only treatment, and lowest in Girdle + Removal treatment both before and after treatment (Fig. 2.6). Differences in spring post-treatment percent cover were consistent across years and treatments, affected by time and treatment but not time*treatment interactions (Appendix D). Lower values across all treatments in spring 2007 indicate that conditions for growth may not have been as favorable in spring 2007 as in spring 2006. Differences in summer percent cover were consistent across years and were affected by time but not treatment or time*treatment interactions (Appendix D).

Woody Seedling Census

Fall seedling counts tended to be less than other seasons, accounting for the loss of individuals over the season, while summer counts tended to be slightly greater than fall numbers, and spring counts were the greatest (Figs. 2.9, 2.10, and 2.11, Appendix C).

Species accounting for the majority of basal area (81.9%) in the pretreatment survey had a variety of responses to treatment. *Q. rubra*, *Q. prinus* and *C. glabra* seedling abundance did not change due to treatment over the course of the study (Fig. 2.9g, f, and b). *Q. rubra* seedling abundance was greater than all other species in fall 2005; however, by fall 2007, *Acer sp.* seedling abundance in the Girdle + Removal treatment and *R. maximum* seedling abundance in the girdle and Girdle + Removal treatments were about the same as *Q. rubra* (Fig. 2.9g, i, and h).

In 2007, *Acer sp.* spring recruitment was high in all treatments, but persisted only in the Girdle + Removal treatment (Figs. 2.11i). *R. maximum* “seedlings”, which included those freely sprouting from roots and those sprouting from stumps and removed after each fall survey, were more abundant in Girdle + Removal treatment plots in 2006 and 2007 than in 2005 (Figs. 2.9h and 2.10h). *B. lenta* seedlings were not present in the surveyed plots.

Four additional species were more abundant in 2007 than 2005 and 2006 in the Girdle + Removal treatment: *Liriodendron tulipifera*, *Hamamelis virginiana*, *Rhododendron calendulaceum*, and *Amelanchier* sp. *(*Figs. 2.9a, d, e, and c; 2.10a, d, e, and f; and 2.11a, d, e, and f).

Woody seedling density is presented with and without *G. ursina*, since stems are right around base height (1.37 m) and may confound the analysis of woody seedling recruitment. However it is important to track the presence of *G. ursina* because it is a dominant Ericaceous understory shrub, found in patches where *R. maximum* is absent, and may be affected by SOD. For fall dates, woody seedling density was affected by time*treatment interactions (Appendix D). Due to the confounding influence of *G. ursina,* Control treatment in fall 2006 and 2007 was significantly greater than Girdle + Removal treatment in all falls (Fig. 2.7). Control treatment in fall 2007 was significantly greater than Girdle Only treatment fall 2005. Woody seedling density without *G. ursina* stems for fall dates was affected by time*treatment interactions (Appendix D). Control treatment in fall 2007 was significantly greater than Girdle Only treatment in fall 2006 (Fig. 2.8). Girdle + Removal treatment in fall 2007 was significantly greater than Girdle Only treatment in all falls. During summer 2006 and 2007, woody seedling density without *G. ursina* was affected by time*treatment interactions but not by treatment (Appendix D). Girdle +

Removal treatment in summer 2007 was significantly greater than Girdle Only treatment in summer 2006 and 2007 (Fig. 2.8).

Chi-square analysis showed that woody species composition differed among treatments for all dates. However, since many expected observations were less than 5 ---an indication the sample size was small--- the chi-square test may not be valid for fall 2005. Woody species composition changed significantly in Girdle Only treatment and Girdle + Removal treatments between summer 2006 and 2007 and in control, Girdle Only treatment and Girdle + Removal treatments between fall dates; however the chi-square test may not be valid for the fall Girdle Only treatment and Girdle + Removal treatment analysis since many expected observations were less than 5.

A meaningful NMS ordination was not found for the seedling count data due to the large number of rare species that make it difficult to distinguish relationships among treatments.

DISCUSSION

Results from the first two years post-treatment demonstrate subtle changes in herbaceous layer vegetation and seedling establishment in the Girdle Only treatment where only the red oaks were girdled and *R. maximum* was left intact. More pronounced changes were observed in the Girdle + Removal treatment where red oaks were girdled and *R. maximum* was cut and removed. Spring herbaceous species richness, summer total species richness and herbaceous layer percent cover were unaffected under either scenario. The hypothesis that woody species richness and seedling density will be affected in the Girdle + Removal treatment before they are affected in the Girdle Only treatment is supported.

As expected, we did not see increases in herbaceous layer species richness, percent cover, or woody seedling density in the Girdle Only treatment; however, estimates of similarity and chi-square analysis picked up on subtle changes. Summer estimates of similarity indicate that the plant community in southern Appalachian forests may change with either scenario of SOD. However, there were no changes in either measure of similarity for fall dates, indicating it may take longer for increased recruitment to be evidenced by seedlings that survive the growing season into fall. Chi-square analysis indicates that woody species composition differed among treatments under both scenarios, however, changes in fall may not be valid due to small sample size.

Acer seedlings increased significantly in Girdle Only and Girdle + Removal treatments. *R. calendulaceum*, *H. virginiana*, *L. tulipifera,* and *Amelanchier* seedling numbers also increased in the Girdle + Removal treatment. *A. rubrum, L. tulipifera*, and *H. virginiana* seeds were identifiable in litter collected for the carbon cycling portion of this study (see Chapter 3). *Acer rubrum* and *L. tulipifera* are early successional species, and their success in the regeneration layer may be due to increased seed production and/or increased germination and establishment in openings created by *R. maximum* removal. *A. rubrum*, *B. lenta*, and *L. tulipifera* seedlings established after chestnut blight and are also expected to successfully recruit due to the loss of *T. canadensis* from HWA (Nelson 1955, Day et al. 1988, Ellison et al. 2005, Elliot and Swank 2008, Nuckolls et al. In Press). *R. maximum* “seedlings” (e.g. suckers) sprouted from stumps in Girdle + Removal treatment despite being removed from the herbaceous layer subplots following each fall survey. We expect in an actual outbreak of *P. ramorum*, sprouts would be subsequently infected and die back, which we simulated by removing them periodically. *C. glabra* and oak species, including *Q. rubra,* and *Q. prinus,* have not yet recruited significantly in either treatment. Oak individuals recorded in the survey are likely established and not new seedlings. However, this is not surprising, since oak recruitment depends on periodic masting that occurs over a longer time scale than the two years observed in this experiment. Fall 2007 was a mast year for oaks, so it is reasonable to expect that further surveys would indicate an increase in oak seedlings.

In the less severe scenario, we expect Q. *rubra* would be lost from the forest. During the first few years after loss of *Q. rubra*, numerous small gaps would open in the forest. Slowly, over decades, *R. maximum* would fill in most gaps, as *R. maximum* inhibit the growth of woody seedlings (Clinton et al. 1994, Beckage et al. 2000). In addition to filling in by *R. maximum*, species that currently comprise the greatest basal area of our study area, including *A. rubrum*, *Q. prinus*, *Carya glabra*,and *Betula lenta*, are poised to increase their size after loss of *Q. rubra* (Appendix B). These species increased in BA in other forest types after chestnut blight (Day et al. 1988, Elliot and Swank 2008). In the forest type studied, *Q. prinus* was codominant (comprising greater than 5% BA) with *C. dentata* at the time of chestnut blight and increased in BA 13.4 % forty years later while *A. rubrum* and *Q. rubra*, which were not codominants prior to chestnut blight, increased by 7.4 and 5.3 %, respectively (Day et. al 1988). Existing *A. rubrum* trees grew in response to defoliation of oaks by gypsy moth and co-occurring oaks, *A. rubrum*, and *B. lenta* grew in response to mortality of *T. canadensis* (Elkinton et al. 2002, Ellison et al. 2005, Nuckolls et al. In Press).

In the southeastern state of Victoria, Australia, dieback caused by a root infection of *Phytophthora cinnamomi* devastated the forest, killing 54% of understory species, including the understory dominant *Xanthorrhoea australis* (grass tree) and canopy dominant *Eucalyptus* species (Weste 1994 and 2003). Species subsequently regenerated when *P. cinnamomi* was less prevalent, probably due to drought that suppressed the pathogen (Weste 2003). Effects of the loss of *R. maximum* due to *P.ramorum* could be similar. The plant community of southern Appalachian forests will quickly change if the high severity scenario occurs. The first few years after loss of *Q. rubra* and *R. maximum* large gaps would open in the forest. Decades later, loss of the dense *R. maximum* cover and associated inhibitory recalcitrant litter could lead to a significant increase in recruitment of woody species, including *A. rubrum*, *H. virginiana*, *Amelanchier sp.*, and *L. tulipifera*, while *R. calendulaceum* would likely dieback due to *P. ramorum* (Clinton et al. 1994, Clinton and Vose 1996, Beckage et al. 2000, and Appendix A). Unfortunately, potential susceptibility of the aforementioned hardwood species to *P. ramorum* complicates our prediction of the possible new species mix (Appendix A). These species will likely suffer non-lethal foliar infection; however, the effect on seedling recruitment is unknown.

P. ramorum is a generalist pathogen and numerous additional species are potentially susceptible to infection and disease (Appendix A). When this study began, *P. ramorum* was not known to infect white oaks, and these species were not manipulated in our experiment. However, a recent study on seedlings indicates that *Q. prinus* and *Q. alba* may be more susceptible, at least as seedlings, than *Q. rubra*, and *Q. prinus* seedlings were more susceptible than *L. densiflorus* and *Q. agrifolia*, coast live oak, that are being devastated in California and Oregon (Garbelotto and Rizzo 2005, Tooley and Kyde 2007). *C. dentata and Fagus grandifolia* in the Fagaceae and *Kalmia latifolia, G. ursina, Rhododendron calendulaceum*, *Vaccinium corymbosum*, and *Oxydendrum arboreum* in the Ericaceae have the potential for infection and mortality (Appendix A). Species in the study area potentially susceptible to foliar infection and stem dieback include: *Acer* species; *Ilex montana;H. virginiana*; *Cornus alterniflora; Sasafras albidum* (in the Lauraceae with *U. califonica*); *L. tulipifera* and *Magnolia* species in the

Magnoliaceae; *Fraxinus pennsylvanica; Amelanchier* species, *Prunus serotina*, and *Rubus* in the Rosaceae; *Clintonia umbellulata* and *Maianthemum* species and possibly others in the Liliaceae; and *Athyrium filix-femina* and *Cystopteris bulbifera*, ferns in the Dryopteridaceae (Appendix A).

Other disturbance factors - wind, logging, fire, and disease- will interact with SOD to determine the future plant community (Douglass and Hoover 1988). Climate change is predicted to alter temperature, precipitation patterns, and storm frequency and intensity and could lead to changes in the forest community composition as well as affecting the spread and pathogenicity of *P. ramorum* and other disturbances with which it interacts (Dale et al. 2001). In areas of the forest where hemlock is present, HWA may eliminate Eastern hemlock while SOD removes oaks, Ericaceous species, and additional susceptible hardwoods. All of these factors need to be considered in planning for management of SOD.

For example, prescribed fire may be an option for SOD management in the southern Appalachians. Areas in California burned at least once since 1950 appear to have resistance to SOD, which is thought to be due to post-fire vegetation composition or soil chemicals unfavorable to *P. ramorum* (Moritz and Odion 2005). Results from a study of dogwood anthracnose, *Discula destructiva*, a fungal pathogen of flowering dogwood, *Cornus florida*, suggest that prescribed fire promotes forest structure and composition that is unfavorable to the disease (Holzmueller et al. 2008). Prescribed fire is being used in southern Appalachian forests to promote oak regeneration and suppress shade tolerant *A. rubrum* and fire intolerant *R. maximum* (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000, Elliot et al. 1999). While prescribed fire may help control *R. maximum* and thus the major potential source of *P. ramorum* innoculum, *A. rubrum* - the species most likely to replace oaks and *R. maximum* lost to SOD- is also suppressed by fire, potentially complicating predictions of changes in the plant community. Prescribed fire may have the added benefit of killing *P. ramorum* spores in soil.

An outbreak of SOD in the southern Appalachians would likely result in non-random species loss of oaks, *Rhododendron* species, other Ericaceous species, and additional species which have been identified as susceptible with uncertain mortality. We expect that in the long-term, species richness, percent cover, and woody seedling density will decrease, as red maple (*Acer rubrum*) successfully colonizes and persists in gaps created by loss of *R. maximum* and *Q. rubra* (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000). Future studies should consider the potential loss of *Q. prinus* and *Q. alba* in addition to *Q. rubra* and *R. maximum*.

Land managers will be faced with the challenge of adjusting to a new species composition in the face of ecological changes arising from SOD. Short-term impacts (e.g. oak cankers and *R. maximum* foliar infection) of the disease will be apparent within a few years of infection, while longer-term effects will arise from the gradual mortality of individual trees and the successive establishment and growth of a new species mix. We do not know how severe or widespread the effects of SOD in the southern Appalachians will be and therefore must prepare contingencies for a number of different scenarios. While SOD infection has been detected in nurseries in the southeastern U.S., the USDA Forest Service Sudden Oak Death National Detection Survey has not found SOD in forests adjacent to nurseries, general forest transects, or in stream baiting in the southern Appalachians (Stokstad 2004, Oak et al. 2007). Forest professionals who notice the tell-tale signs of cankers and leaf blight should quickly contact local authorities (USDA Forest Service, USDA Animal and Plant Health Inspection Service, or other local plant pathogen specialists) to test suspect plants. Any initial outbreak will need to be contained by following established guidelines to prevent its spread, such as removal and burning of infected plants as has been practiced in Oregon (Goheen et al. 2002). Current and future monitoring to detect infection and to collect data on community responses is essential to make appropriate management decisions.

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TABLES

Table 2.1 Calendar of field measurements and experimental treatment.

	Summer 2005	Fall 2005	Winter 2005-6	Spring 2006	Summer 2006	Fall 2006	Spring 2007	Summer 2007	Fall 2007
Tree and shrub survey	X								
Understory richness & cover	X			X	X		X	X	X
Understory seedling count		X				X	X	X	X
Canopy light interception		X							
Girdling and *R. max* removal			X						

Table 2.2 Pre-treatment basal area and density by treatment. *Q. rubra* and *R. maximum* are listed separately in addition to totals for each treatment block.

	Basal Area (m^2ha^{-1})						Number of stems ha^{-1}					
Treatment	Total (SD)		Trees (SD)		Shrubs (SD)		Total (SD)		Trees (SD)		Shrubs (SD)	
Control	40.2	(7.5)	35.0	(4.1)	5.2	(3.4)	5737	(1857)	619	(293)	5119	(1564)
Q. rubra	10.1	(2.9)	10.1	(2.9)	0.0	(0.0)	126	(55)	85	(13)	41	(61)
R. max	4.9	(5.6)	1.8	(2.7)	3.1	(2.9)	1856	(930)	148	(219)	1707	(745)
Girdle	35.1	(13.0)	31.8	(11.2)	3.3	(1.9)	3807	(1201)	348	(61)	3459	(1240)
Q. rubra	9.6	(3.0)	9.5	(2.9)	0.0	(0.1)	63	(45)	56	(33)	7	(13)
R. max	2.5	(0.5)	0.3	(0.6)	2.1	(0.7)	1804	(246)	33	(58)	1770	(230)
Girdle + Removal	34.6	(10.4)	31.4	(9.9)	3.2	(0.7)	3630	(1161)	356	(88)	3274	(1104)
Q. rubra	13.3	(6.6)	13.3	(6.6)	0.0	(0.0)	70	(39)	67	(40)	4	(6)
R. max	2.1	(0.1)	0.3	(0.3)	1.7	(0.4)	1452	(265)	30	(28)	1422	(290)

FIGURES

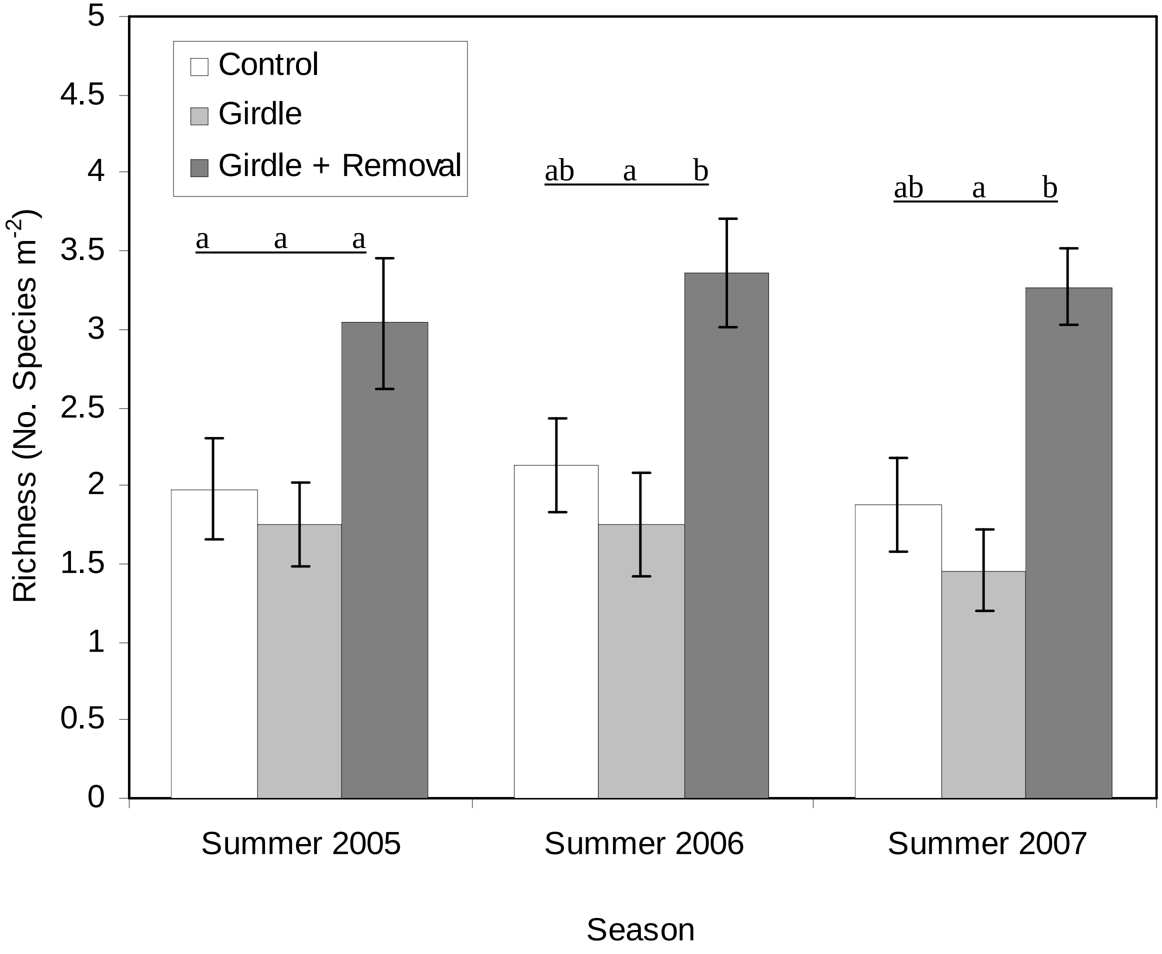

Figure 2.1 Species richness by season before and after treatment for all species.

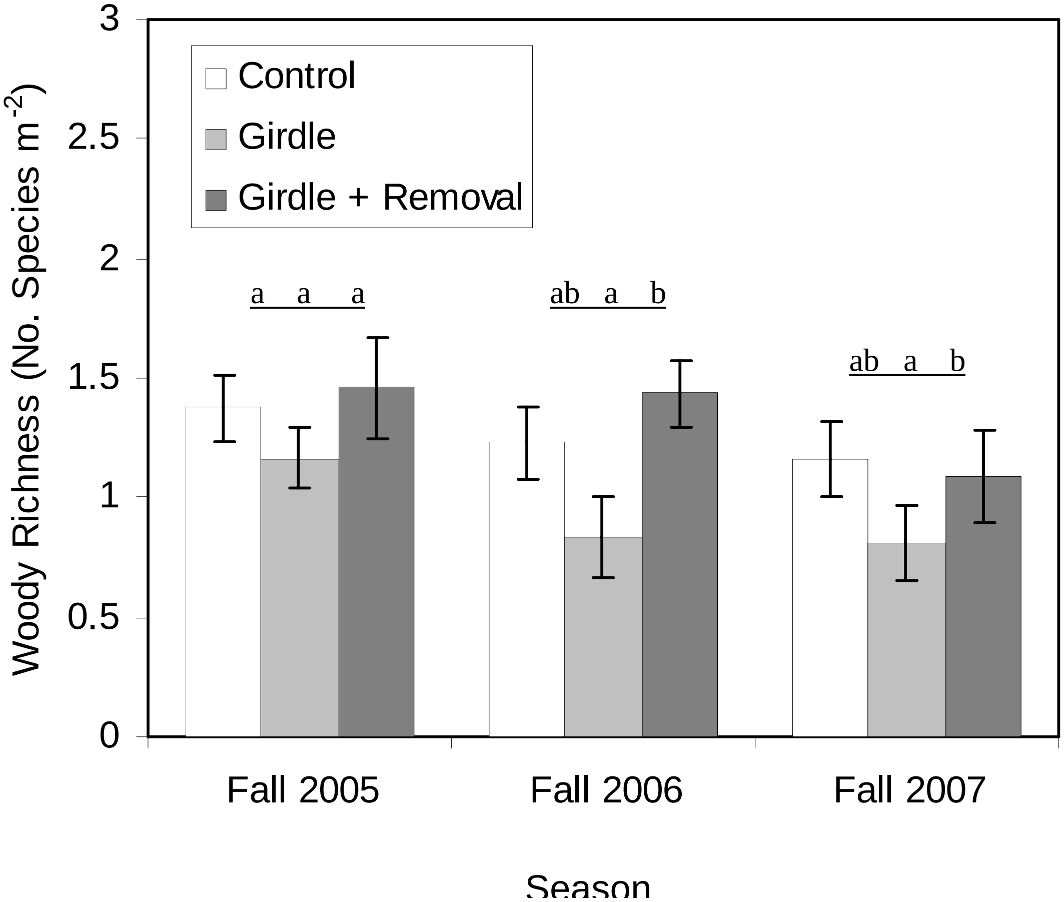

Figure 2.2 Species richness by season before and after treatment for woody species.

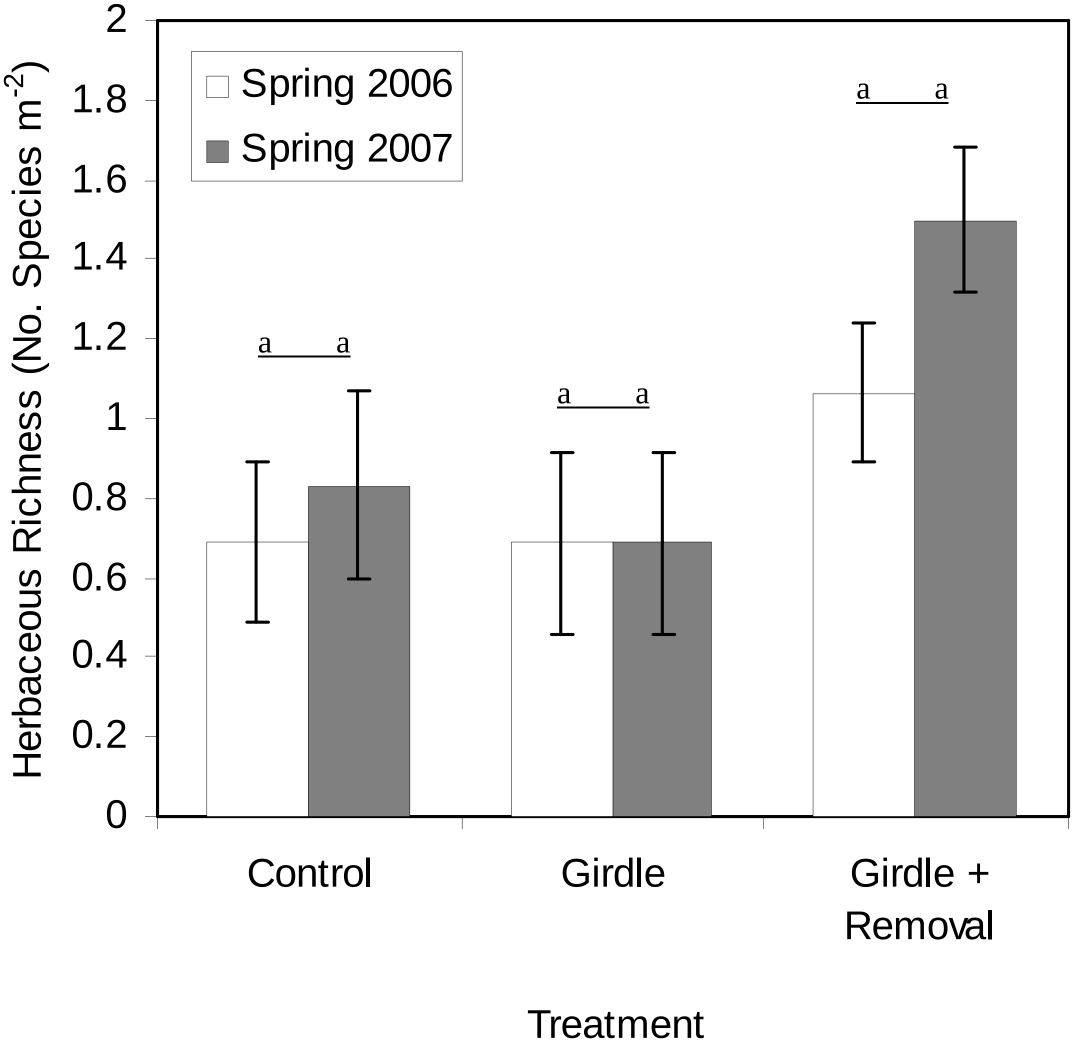

Figure 2.3 Herbaceous species richness by treatment.

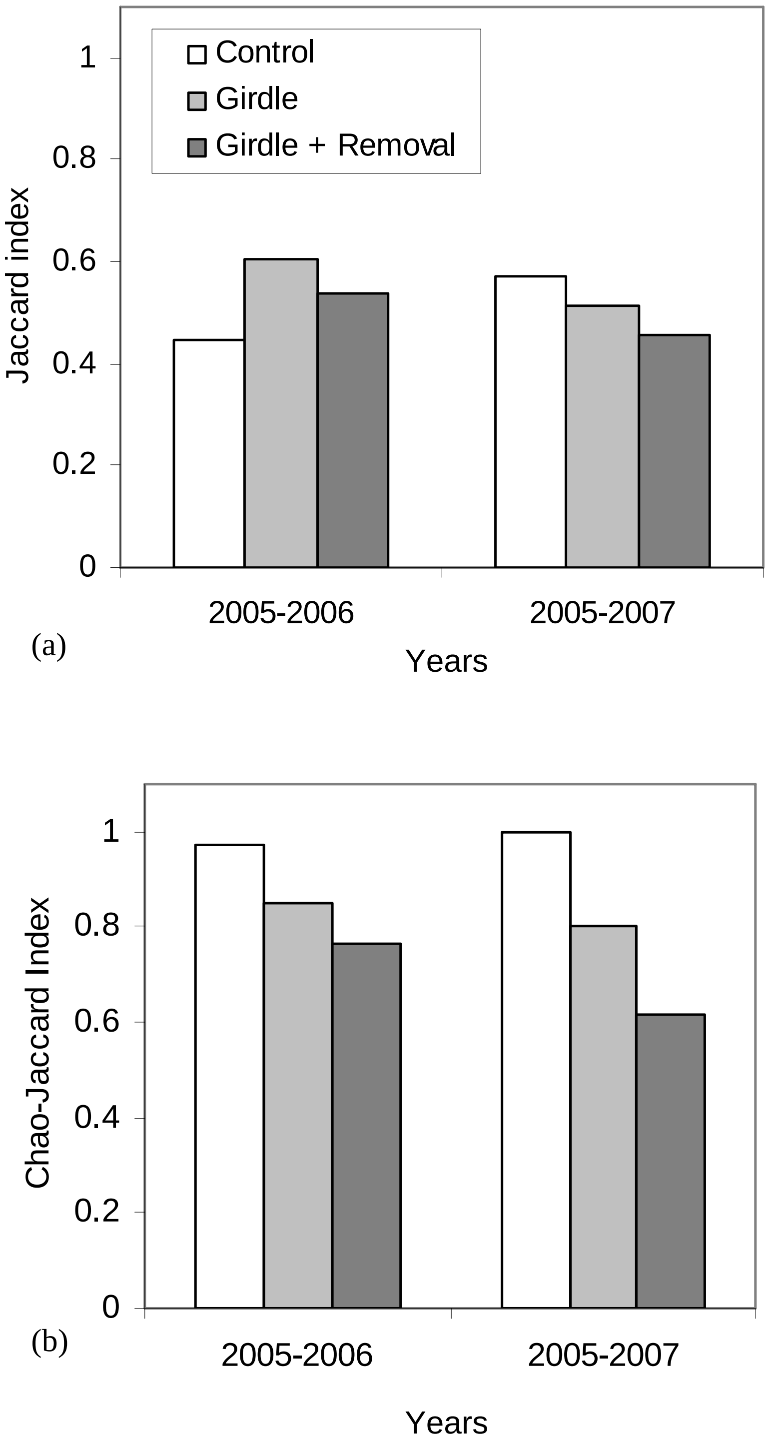

Figure 2.4 Summer similarity indices. (a) Classic Jaccard and (b) Chao-Jaccard indices for pretreatment versus one year post-treatment and pretreatment versus two years post-treatment.

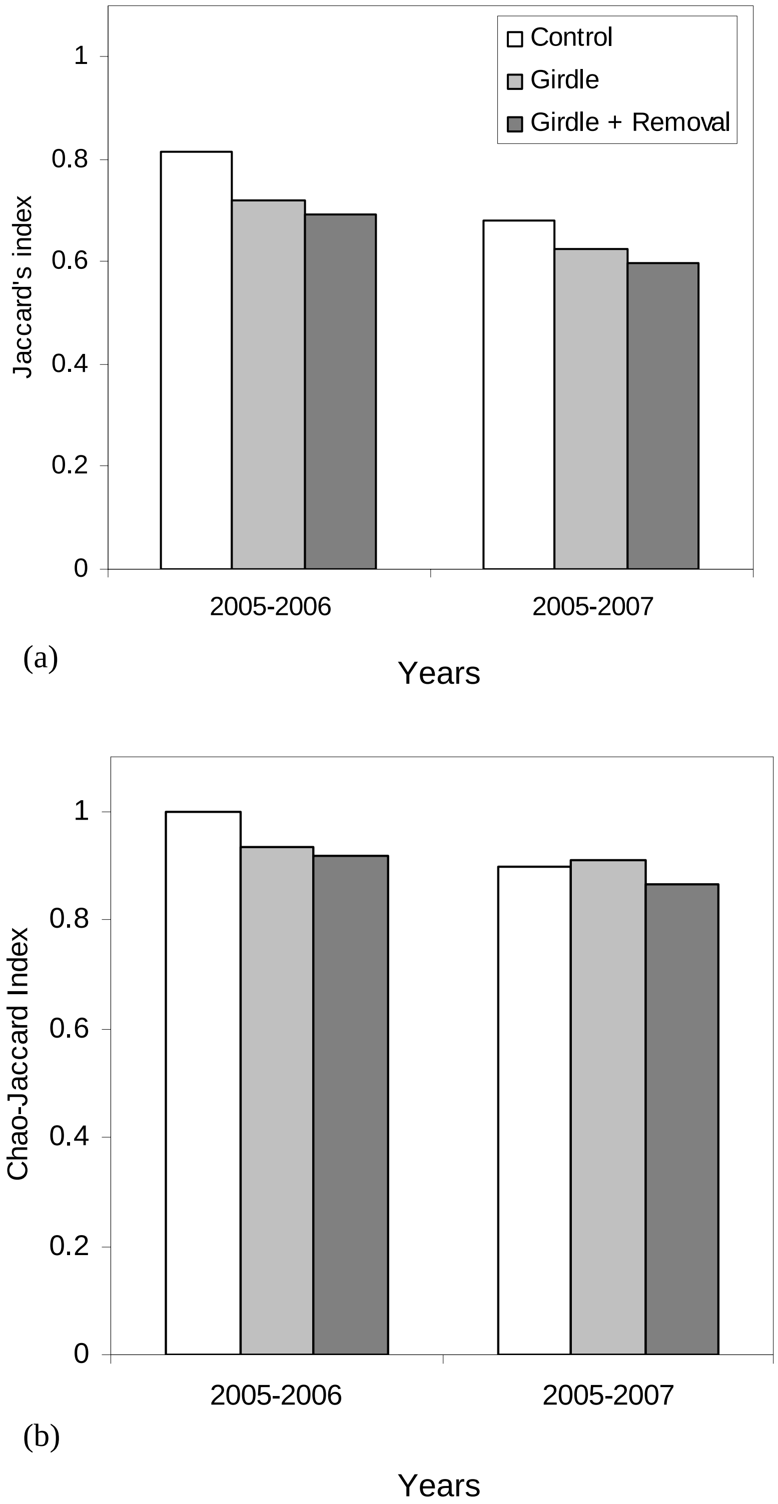

Figure 2.5 Fall similarity indices. (a) Classic Jaccard and (b) Chao-Jaccard indices for pretreatment versus one year post-treatment and pretreatment versus two years post-treatment.

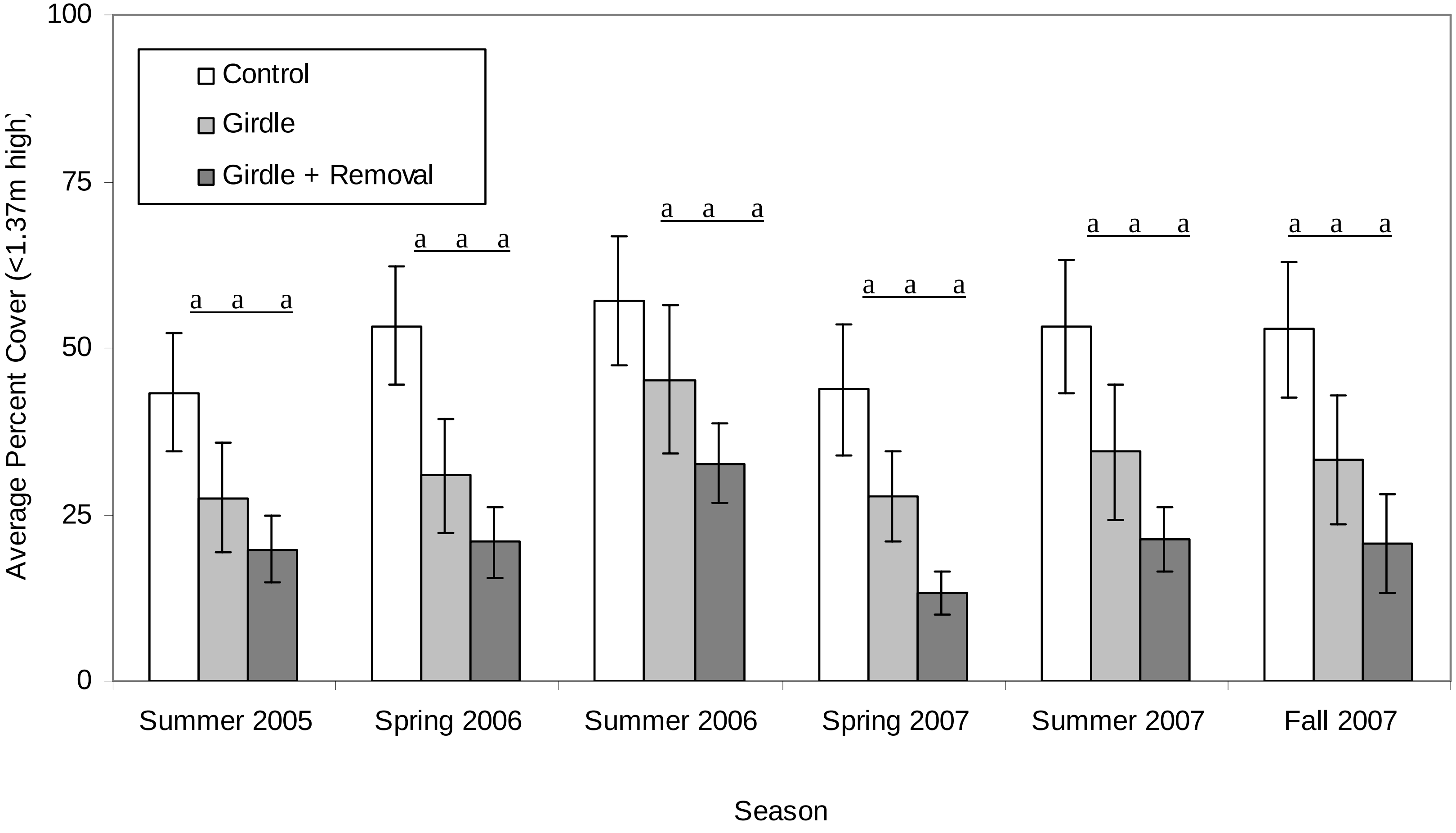

Figure 2.6 Total percent cover by season before and after treatment.

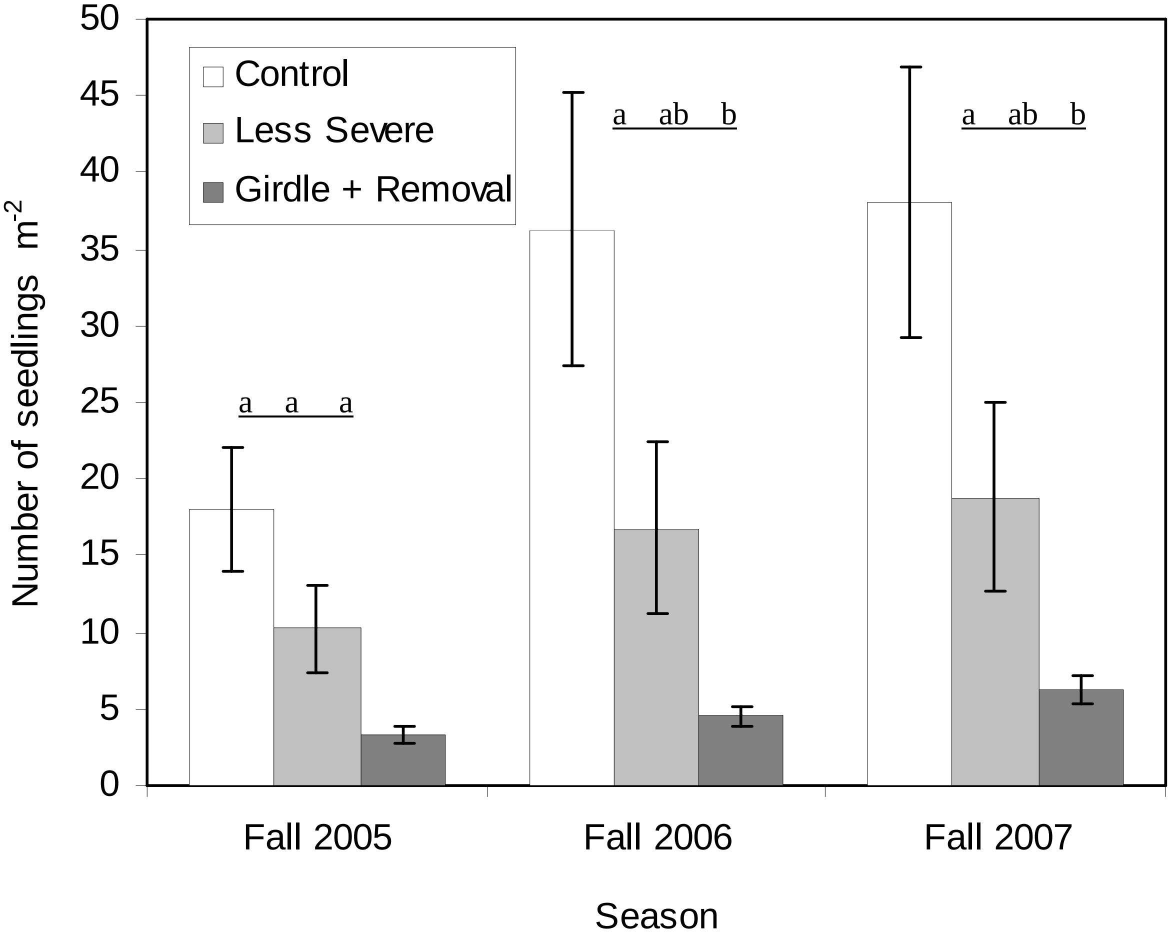

Figure 2.7 Total woody seedling density before and after treatment by season.

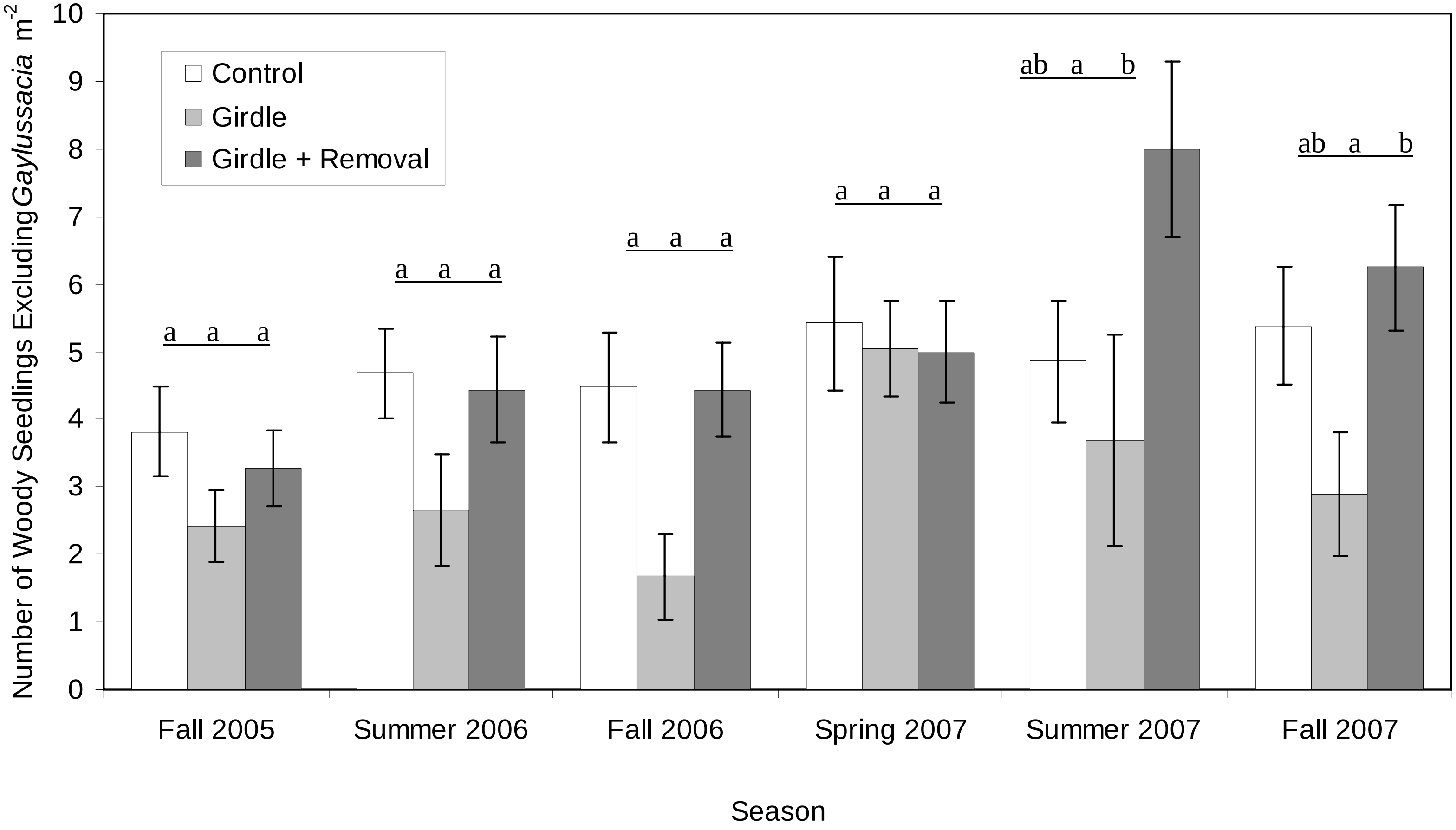

Figure 2.8 Woody seedling density excluding *G. ursina* before and after treatment by season. *G. ursina* was not counted in spring or summer and is omitted from this graph.

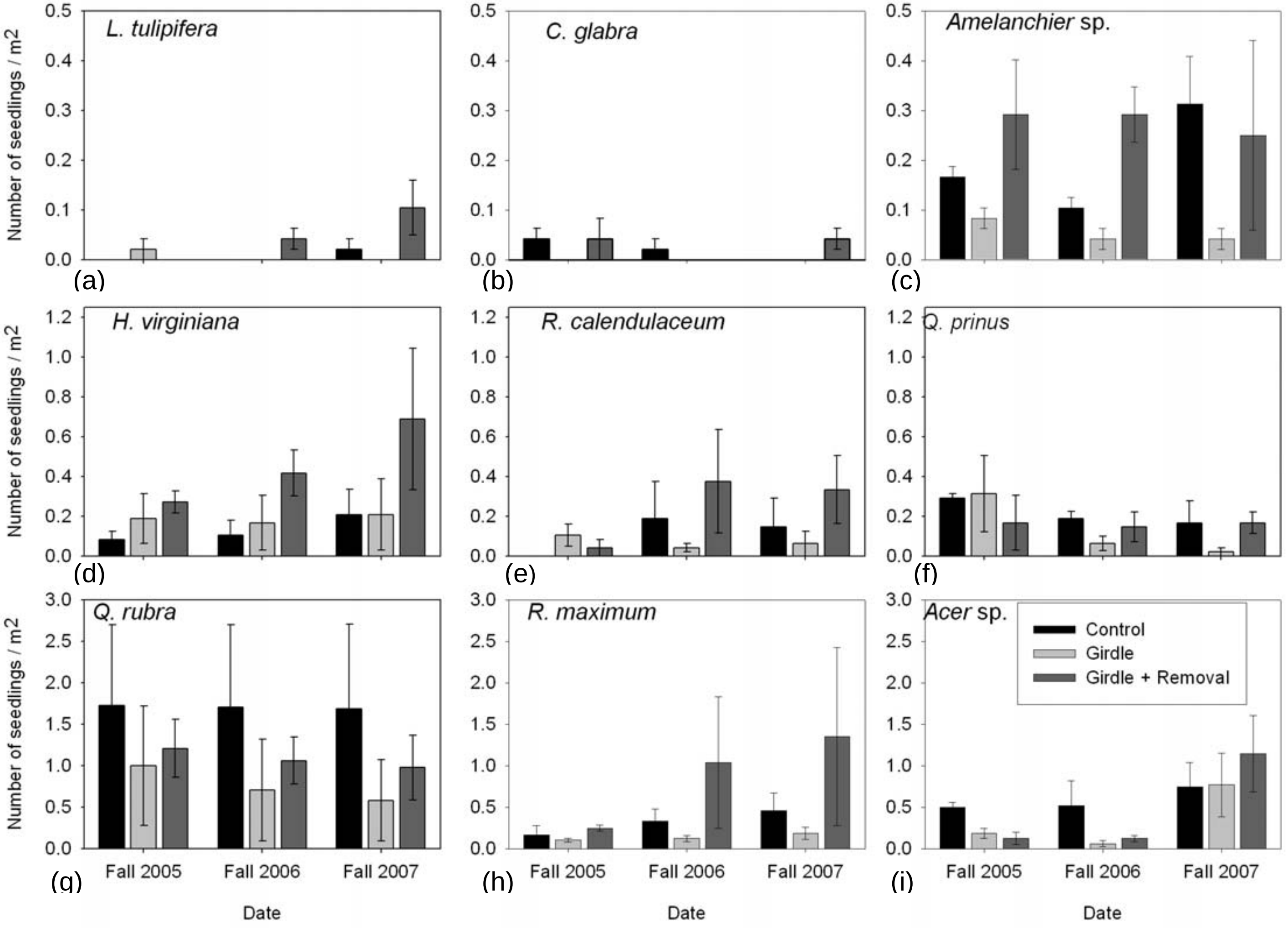

Figure 2.9 Fall abundance of woody seedlings. Species include: (a) *L. tulipifera*, (b) *C. glabra*, (c) *Amelanchier* sp., (d) *H. virginiana*, (e) *R. calendulaceum*, (f) *Q. prinus*, (g) *Q. rubra*, (h) *R. maximum*, and (i) *Acer* sp. NOTE: Due to a wide range of values, scales differ between horizontal rows.

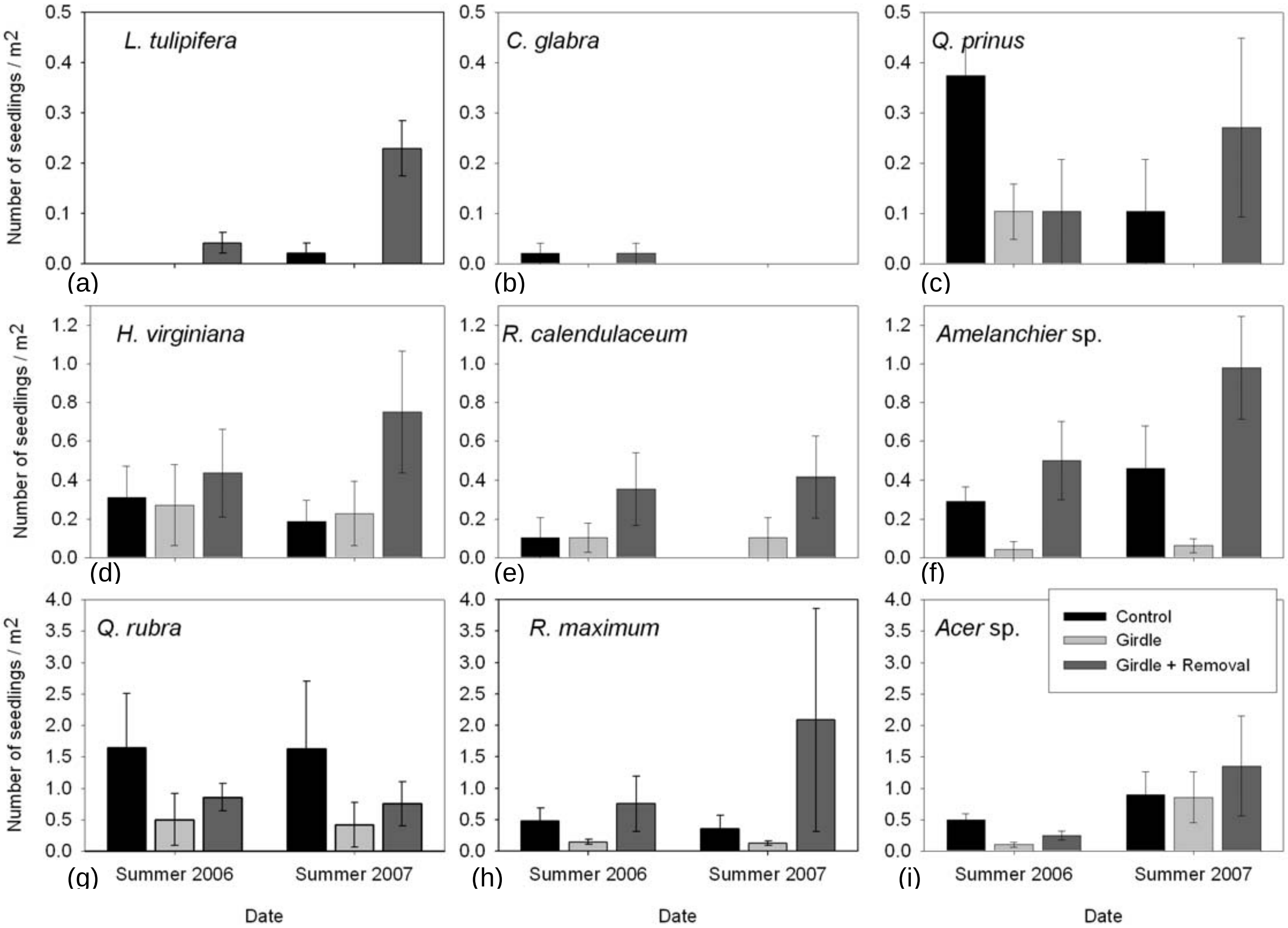

Figure 2.10 Summer abundance of woody seedlings. Species include: (a) *L. tulipifera*, (b) *C. glabra*, (c) *Q. prinus*, (d) *H. virginiana*, (e) *R. calendulaceum*, (f) *Amelanchier* sp., (g) *Q. rubra*, (h) *R. maximum*, and (i) *Acer* sp. NOTE: Due to a wide range of values, scales differ between horizontal rows.

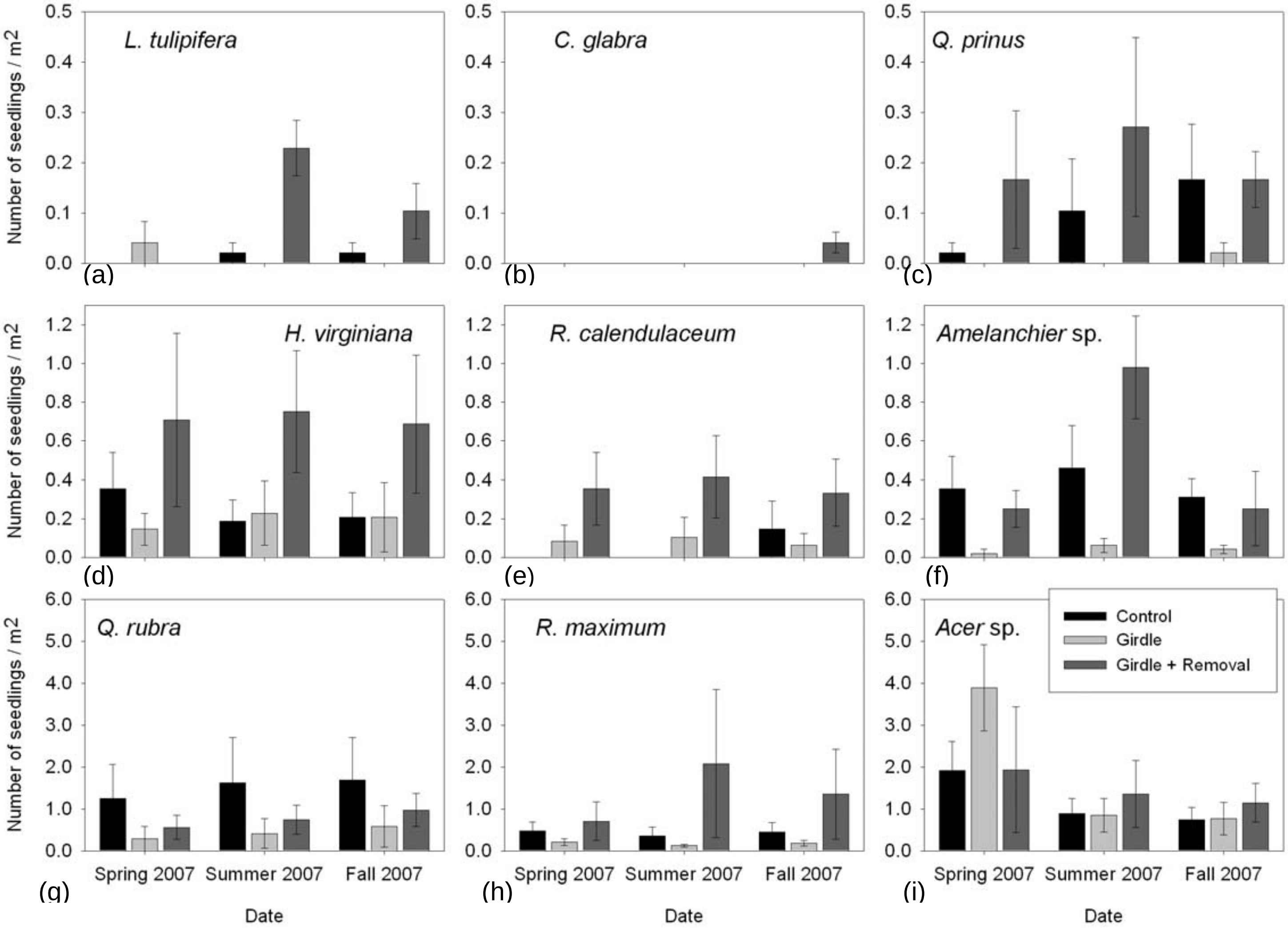

Figure 2.11 Spring, summer, and fall 2007 abundance of woody seedlings. Species include: (a) *L. tulipifera*, (b) *C. glabra*, (c) *Q. prinus*, (d) *H. virginiana*, (e) *R. calendulaceum*, (f) *Amelanchier* sp., (g) *Q. rubra*, (h) *R. maximum*, and (i) *Acer* sp. NOTE: Due to a wide range of values, scales differ between horizontal rows.

CHAPTER 3

POTENTIAL EFFECTS OF SUDDEN OAK DEATH ON LITTER COMPOSITION AND SOIL TEMPERATURE, MOISTURE, AND RESPIRATION OF A MESIC OAK FOREST IN THE SOUTHERN APPALACHIANS[1]

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[1] Watkins, M. H. M. and R. L. Hendrick. To be submitted to *Forest Ecology and Management.*

ABSTRACT

The causal agent of sudden oak death (SOD), *Phytophthora ramorum*, is expected to eventually invade forests in the southern Appalachians. Dominant overstory, *Quercus rubra* L., and understory, *Rhododendron maximum* L., species are susceptible to the pathogen and may be affected by SOD. The objective of this study was to quantify the effects of simulated SOD on litterfall and soil temperature, moisture, and respiration under two possible scenarios: (1) a moderate severity outbreak of SOD with high mortality of northern red oak, Q. *rubra*, only (Girdle Only) and (2) a high severity scenario in which the *R. maximum* understory would be severely impacted in addition to *Q. rubra* (Girdle + Removal). In the first two years post-treatment, litterfall in both scenarios was as expected: due to aboveground loss of biomass there was more litterfall in the Girdle Only treatment and less litterfall in the Girdle + Removal treatment, which simulated a later stage of SOD when *R. maximum* litter would no longer be contributed. As expected, soil temperature was slightly greater in the Girdle + Removal treatment than in the Control or Girdle Only treatments; however soil moisture did not decrease and was similar to Control in both scenarios. While there was no significant effect on soil respiration in the Girdle Only treatment, lower soil respiration only in the Girdle + Removal treatment suggests *R. maximum* removal created large, persistent belowground root gaps, indicative of an overall decrease in root and microbial production respiration rather than an increase in decomposition respiration due to greater litter input from dead roots and increased temperature.

INTRODUCTION

Phytophthora ramorum (Werres, De Cock and Man in't Veld), an oomycete fungus in the Kingdom Stramenopila, spreads by spores, affects only aboveground plant parts, and infects a broad range of species including red oaks (*Quercus,* section *Lobatae*) and woody species in the family Ericaceae. It was first described as a pathogen on *Rhododendron* spp. in Germany (Werres et al. 2001), however recent research based on ecological niche modeling places the origin of *P. ramorum* as eastern Asia (Kluza et al. 2007). Foliar and stem infection of nursery and garden specimens of *Rhododendron catawbiense* Michx., a species native to the southern Appalachians, has led to mortality in Europe (Werres et al. 2001). Sudden oak death (SOD), of which initial outbreaks in the mixed hardwood forests of California caused “sudden” unexplained mortality of oaks (*Quercus* spp.) and tanoak (*Lithocarpus densiflorus* [Hook. & Arn.] Rehd.), is now identified as an infection by *P. ramorum* from central California to southern Oregon (Werres et al. 2001, Rizzo et al. 2002a, Rizzo et al. 2002b, Goheen et al. 2002, Rizzo and Garbelotto 2003, Garbelotto and Rizzo 2005). It reached epidemic levels in central California and killed tens of thousands of trees (Rizzo et al. 2002a, Rizzo et al. 2002b, Goheen et al. 2002, Rizzo and Garbelotto 2003, Garbelotto and Rizzo 2005). A broad range of plant species, from ferns to redwoods, have tested positive as carriers of *P. ramorum* (Garbelotto and Rizzo 2005). Non-lethal infection of California bay laurel (*Umbellularia californica*), a dominant understory shrub, has created a persistent source of innoculum in soil and water (Maloney et al. 2005, Davidson et al. 2005, Fichtner et al. 2007).

Ecological and climate models suggest that climate and species composition make southeastern U.S. forests highly susceptible to infection (Kluza et al. 2007, Venette and Cohen

2006). Numerous herbaceous and woody species, particularly red oaks and Ericaceous species, are susceptible to infection with varying degrees of expected disease effects and mortality. Of particular interest in the southern Appalachians is the likely susceptibility of oaks, specifically northern red oak (*Quercus rubra*) and rosebay rhododendron (*Rhododendron maximum*, a close relative of *R. catawbiense*). Shipments of azaleas (*Rhododendron* spp.) and camellias (*Camellia* spp.) from California nurseries to the southeastern U.S. have contained *P. ramorum* and it is highly likely that SOD will eventually spread to southeastern U.S. forests (Stokstad 2004).

Early pathogenicity testing indicated that *Q. rubra* and *R. maximum* are susceptible in vitro to *P. ramorum* (Werres et al. 2001, Tooley et al. 2004). Both *Q. rubra* and *R. maximum* are expected to experience some degree of mortality due to SOD based on reports of disease in Europe (Werres et al. 2001 and Brasier et al. 2004). Foliar and stem infection of nursery and garden specimens of *Rhododendron catawbiense* Michx. (Catawba rhododendron, a southern Appalachian native and close relative of *R. maximum*) has led to mortality in Europe (Werres et al. 2001). Horticultural specimen *Q. rubra* trees in Europe developed canker infection at the trunk and SOD progressed as in other oaks and tanoaks, eventually girdling the tree and causing mortality (Brasier et al. 2004). *R. maximum* is expected to develop a foliar infection, as have rhododendrons in Europe, with effects anywhere from a persistent non-lethal infection, as occurs in California bay laurel, to a fatal disease, as with European rhododendrons (Maloney et al. 2005, Davidson et al. 2005, Fichtner et al. 2007, Werres et al. 2001).

Introduced forest pests and pathogens have been common in the southern Appalachians since European colonization. Chestnut blight (*Cryphonectria parasitica*) reduced the once dominant overstory American chestnut (*Castanea dentata*) to a minor species in the shrub layer of the forest (Day et al. 1988, Ellison et al. 2005). The hemlock wooly adelgid (*Adelges tsugae* Annand; HWA) is presently spreading rapidly in the southern Appalachians and threatens to eliminate Eastern hemlock (*Tsuga canadensis*) (Brown 2004, Ellison et al. 2005). SOD will likely also result in non-random species loss, potentially changing the structure of the plant community and affecting ecosystem processes.

Changes in plant community structure and diversity due to disturbance have the potential to affect ecosystem production, decomposition, and nutrient cycling, which, in turn, determine plant species composition (Chapin et al. 2002b, Wardle 2002.). The severity of SOD impact in the forest will depend on the timeframe of infection and progression of disease, the actual mortality of trees and shrubs, and the resistance and resilience of the plant community. Based on previous studies, we expect the loss of *Q. rubra* and *R. maximum* would result in an initial pulse of leaf and woody litter aboveground and an increase in belowground root litter via root death (Schroeer et al. 1999, Nuckolls et al. In Press). After the initial pulse in litter, plant productivity would temporarily decrease due to lack of vegetation in gaps created above- and belowground. In the case of loss of *Q. rubra* alone, productivity would recover relatively quickly by existing vegetation filling in gaps; however, if both *Q. rubra* and *R. maximum* are lost, productivity would take longer to recover due to the extensive loss of vegetation (Schroeer et al. 1999). Eventually, other hardwood species such as *A. rubrum* would replace *R. maximum* and *Q. rubra* lost to SOD (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000). A severe outbreak of SOD would lead to the replacement of recalcitrant, high lignin: nitrogen (N) *R. maximum* and *Q. rubra* litter by other litter, potentially increasing soil pH, N availability, and labile soil carbon (C), leading to an increased rate of decomposition. Over the long-term, the shift in litter quality (i.e. lower C:N, higher quality) would lead to a change in the soil microbial community, which would transform from a recalcitrant system dominated by mutualistic mycorrhizal fungi to a more fertile bacteria dominated assemblage (Wardle 2002).

Disturbance may directly disrupt soil or indirectly alter litterfall quality and quantity, and the effects of disturbance on soil organisms can be inferred by observing changes in soil respiration (Chapin et al 2002b, Vose and Bolstad 2007). Soil respiration reflects the combined biological activity of autotrophic and heterotrophic soil organisms and is measured as the rate of CO_2 evolved from the soil, often referred to as soil CO_2 efflux (Coleman et al. 2004b). About half of soil respiration is contributed by decomposer organisms processing detritus and the remaining half is from living plant roots, their mycorrhizal fungi and other root-associated microbes, with soil fauna and free living microbes contributing a nominal amount (Kuzyakov 2006, Högberg and Read 2006). Disturbance can alter soil respiration via changes in soil temperature and moisture, which are considered the most influential factors on soil CO_2 efflux. (Vose et al 1995, Bolstad and Vose 2005). Logging in southern Appalachian forests temporarily decreases soil respiration, which recovers over time if the forest regrows, but if forests are converted to pasture, soil respiration is set at a new, lower rate (Bolstad and Vose 2005, Vose and Bolstad 2007). Litter exclusion has been shown to reduce soil respiration in the southern Appalachians and girdling of *Tsuja canadensis* reduced soil CO_2 efflux in the first two years after treatment (Reynolds and Hunter 2001, Nuckolls et al. In Press). SOD is expected to lower soil respiration by altering litterfall and soil temperature and moisture, and, depending on the severity of its effects, could reset the forest to a new, lower, rate of average soil respiration.

The objective of this study was to quantify the effects of simulated SOD on aboveground litterfall and on soil temperature, moisture, and respiration under two possible scenarios. Under the first scenario, *Q. rubra* were girdled to simulate a moderate severity SOD outbreak with high mortality of red oaks only. The high-severity scenario treatment, with red oaks girdled and *R. maximum* cut and removed from the site simulated the loss of both red oak and rhododendron, with the concomitant loss of aboveground biomass and litter input. We expected to see evidence of increased litterfall in the Girdle Only treatment as a stress response to girdling and a lack of *R. maximum* litterfall in the Girdle + Removal treatment. We hypothesized that girdling red oaks and removing *R. maximum* would (1) create aboveground gaps that would result in more energy reaching the forest floor, resulting in an increase in surface soil temperature and a decrease in surface soil moisture; and (2) increase belowground litter from dead fine roots and decrease carbon available to roots and microbes. Initial increases in temperature and fine root litter would tend to increase soil respiration; however, a decrease in soil moisture and carbon resources would outweigh increases in temperature and fine root litter and result in overall lower soil respiration. We expected effects on temperature, moisture, and soil respiration to be most evident in the Girdle + Removal treatment and expected limited treatment effects on temperature, moisture, and soil respiration in the Girdle Only treatment due to gradual mortality of *Q. rubra* and because belowground gaps created by girdling *Q. rubra* are expected to be less extensive and ephemeral compared to the extent and severity of belowground gaps created by *R. maximum* removal. Belowground root gaps were not detected in a previous study of girdling in slash pine (*Pinus elliotii* Engelm.) due to the rapid response of understory ground cover (Schroeer et al. 1999).

METHODS

Site Description

The study area, located at Coweeta Hydrologic Laboratory in the Nantahala Mountains of western North Carolina (35°02' N, 83°27' W), is characterized by a mesic oak (formerly oak-chestnut) forest with an oak overstory and either a rich herbaceous layer or patches of thick *R. maximum* in the understory which suppress herbaceous species (Day et al. 1988). Red oak lumber is valued for furniture and flooring and *Q. rubra* acorns are a major food source for wildlife, including white tailed deer, wild turkey, and black bears (de Steiguer et al. 1989, Kirkpatrick and Pekins 2002). *Q. rubra* and *R. maximum* could lose dominance in the forest canopy if affected by an outbreak of SOD (Davidson et al. 2003).

The research plots are located at an elevation of 1200 m in a mixed hardwood forest with a significant understory of *R. maximum* and a northerly aspect. Mean annual precipitation is approximately 1800 mm, and is generally distributed evenly throughout the year (USFS 2008). Total annual precipitation at the Coweeta Hydrologic Laboratory climate station was 1549.6 mm in 2006 and 1212.9 mm in 2007 (USFS 2008). Mean annual air temperature is approximately 13 °C and ranges from -18 °C to 24 °C (Swift et al., 1988). Mean annual air temperature at the Coweeta Hydrologic Laboratory climate station was 14.1°C in 2006 and 14.3°C in 2007 (USFS 2008). Soil characteristics are typical for highly weathered Ultisols, being relatively high in organic matter and moderately acidic with both low cation exchange capacity and low percent base saturation (Swank and Crossley 1988).

Experimental Design

During winter 2004-2005, nine experimental plots (25 m x 25 m) were established in stands containing at least 15% *Q. rubra* basal area and with *R. maximum* patches covering at least 15% of the plot area. Eight plots are located around a central large *Q. rubra* tree, and one plot is located around a central large *Nyssa sylvatica* surrounded by three smaller *Q. rubra* trees. Plots were matched based on similarity of overstory composition and treatments randomly assigned in a complete block design. In each of three blocks, one plot was assigned to each of three treatments described below in Treatment Application.

Overstory and Understory Survey

The pretreatment vegetation survey occurred in summer 2005 (Table 1). On each plot, all trees greater than 10 cm diameter at breast height (DBH = 1.37 m) were identified to species, tagged, and measured. All shrubs greater than 1 cm DBH were identified to species and recorded by size class. Basal area (BA) and density were calculated for trees and shrubs on each plot.

In fall 2005, percent canopy cover was estimated using a spherical densiometer (Table 1). Measurements were taken at 18 locations across each plot: 9 points along transects (3 points on 3 transects at roughly 10 m intervals, beginning at 5 m into the plot and running roughly along the contour parallel to the top and bottom) and at the 9 sampling points established for soil temperature, moisture, and respiration. On one plot a transect point overlapped with one of the sampling points, so that plot had only 17 locations. Percent canopy cover was estimated at each location as the average of measurements taken in four cardinal directions.

Thirty four woody species were identified in the pre-treament survey (Appendix B). Total pre-treatment basal area of trees and shrubs was similar across treatments, ranging from 34.6 to 40.2 m^2 ha^{-1} (Table 2, Appendix B). *Q. rubra* basal area ranged from 9.6 to 13.3 m^2 ha^{-1} while *R. maximum* basal area was between 2.1 and 4.9 m^2 ha^{-1}. *Q. rubra* comprised an average of 30.3% of pretreatment BA, followed by *A. rubrum* at 21.0%, *Q. prinus* at 17.2%, *R. maximum* at 8.4%, *Carya glabra* at 5.0%, and *Betula lenta* at 4.4%, together accounting for 86.3% basal area (Appendix B). Pre-treatment stem density was greater in control than treatment plots, due to a single plot having a large number of small diameter stems (Table 2, Appendix B). Pre-treatment estimated canopy cover was similar across treatments and ranged from 83.4 % (sd = 8.7) in plots assigned the Girdle + Removal treatment to 87.4 % (sd = 9.5) in plots assigned the Girdle Only treatment and 86.1 % (sd = 9.4) in plots assigned to Control (see Treatment Application below for description of treatments).

Treatment Application

In each block, one plot was randomly assigned to each of the three treatments: (1) Control, (2) *Q. rubra* girdled (Girdle Only), and (3) both *Q. rubra* girdled and *R. maximum* cut and removed (Girdle + Removal). The girdling of *Q. rubra* and removal of *R. maximum* was conducted in February 2006 (Table 1). Trees were girdled with a chainsaw by cutting through the cambium of *Q. rubra* at the base of the tree. *R. maximum* trunks were cut at the ground level on most plots. To simulate a later stage of SOD, when *R. maximum* litter would no longer be contributed and seedlings would not be shaded, cut *R. maximum* limbs and trunks were manually removed from treatment 3 plots; however, several large pieces of *R. maximum* stems were limbed but left on one plot due to time constraints. The litter layer on *R. maximum* removal plots was disturbed as little as possible; however, some disturbance was unavoidable and was consistent across plots. *R. maximum* stumps resprouted during the growing season and emerging stems and leaves were periodically removed to simulate continued stress from belowground damage as well as reinfection by *P. ramorum*.

Litterfall

In fall 2005, four 1m^2 traps were installed randomly at each plot. Litter was collected between September 2006 and December 2007. Samples were collected weekly during leaf drop between September and November and monthly at all other times. All litter was dried at 60ºC for at least 72 hours.

Samples from September 2006 through March 2007 were sorted into the following categories: red oaks (*Q. rubra* and possibly *Quercus velutina*, black oak, from trees adjacent to the plot), *R. maximum* and mountain laurel (*Kalmia latifolia)*, other leaves (including *A. rubrum*, *Q. prinus*, *Q. alba*, and other species listed in Appendix A), other plant material (e.g. twigs, woody material, bark, seeds, flowers), and miscellaneous (including animals and unidentifiable material). Dried red oak leaves are easy to distinguish from other oaks by their pointed lobes; however they are difficult to distinguish from one another, thus all red oak leaves were lumped. *K. latifolia* was included with *R. maximum* because, as dried leaves, they are indistinguishable and because they have similar physical and chemical properties and thus similar effects on the soil. Sorted litter samples were weighed to the nearest tenth of a gram.

Soil Temperature, Moisture, and Respiration

Nine sampling points were marked in each plot by short lengths of 1.9 cm diameter PVC pipe driven into the ground, such that they represented all areas of each plot: three located under rhododendron patches, three under red oak canopies, and three under other tree canopies or in the open. Each time samples were taken, the litter layer was removed from each sampling point prior to measurement. Post-treatment soil temperature at 20 cm depth and bare soil respiration (CO_2 efflux) were measured biweekly during the growing season, late April to November 2006 and May to September 2007, using a LICOR 6400 portable Infrared Gas Analyzer (IRGA) (LI-COR Inc, Lincoln, NE). Soil moisture of the top 15 cm was measured using time domain reflectometry (Field Scout TDR 100, Spectrum Technologies, Inc.).

Soil respiration was normalized for temperature based on the average soil temperature per sampling period (samples were taken over two or three successive days) via a Q_{10} equation and will be referred to as temperature-corrected soil respiration (3.1).

$$y = \text{soil } CO_2 \text{ efflux } (2\text{\^{} }(\text{average soil temperature-measured soil temperature})/10) \tag{3.1}$$

Correcting soil respiration for temperature reduces temperature variability within a sampling period (over the course of a few days in this study) and eliminates temperature as a confounding factor.

Statistical Analysis

Statistical analyses were based on a randomized complete block design with three blocks in which one plot in each block was assigned to each of the three treatments: Control, Girdle Only, and Girdle + Removal. One way analysis of variance (ANOVA) was calculated for litterfall. Effects of litter category, treatment, and litter category*treatment were calculated and Tukey's Studentized Range (HSD) Test was used to determine differences between treatments and litter category*treatment. One way repeated measures ANOVA was calculated for soil temperature, moisture, and and respiration (both standard temperature corrected) with a mixed model. Effects of time, treatment, cover time*treatment, time*cover, and time*treatment*cover were calculated for soil temperature, moisture, and respiration (both standard temperature corrected), as well as effects of temperature and moisture on soil respiration. Multiple comparisons were calculated with one way ANOVA. All tests were evaluated for significance at alpha = 0.05.

RESULTS

Litterfall

There was a significant interaction of litter category and treatment (Appendix E). Girdle Only plots contained the greatest average amount of total litter (272.4 gm^{-2}, SD= 15.6), Control plots an intermediate amount (230.8 gm^{-2}, SD = 21.3), and Girdle + Removal treatment the least (147.8 gm^{-2}, SD = 8.6). Other leaves comprised the greatest average amount (Fig. 3.1) and the greatest percentage (Fig. 3.2) of litter in all treatments. Girdle Only treatment contained the greatest average amount of red oak and other plant material. A closer inspection of other plant material showed it was mostly seeds and flowers in the first two sampling dates (September 25 and October 7 2006), with slightly more in Girdle Only treatment than the Girdle + Removal treatment and Control (Figs. 3.3, 3.4, and 3.5). Twigs made up the majority of other plant material for late October through March, with Girdle Only treatment having more than five times the woody litter of Control and Girdle + Removal treatment on all dates except March, when Control had almost twice as much woody litter as Girdle Only. The average amount of *Rhododendron* and *Kalmia* litter was less than 1 g/m^{-2} (0.3 g/m^{-2}, SD = 0.1) in Girdle + Removal treatment, while Girdle Only treatment had 34.2 g/m^{-2} (SD = 10.0) and Control treatment 16.1 g/m^{-2} (SD = 7.4) (Fig. 3.1). Miscellaneous litter was less than 3 g/m^{-2} in all treatments (Fig. 3.1).

Soil Temperature, Moisture, and Respiration

Soil temperature was affected by time*treatment*cover interaction. The Girdle + Removal treatment soil temperature was significantly greater than Control treatment in 6 out of 13 dates in 2006 (mid June, early July, mid July, late July, mid August, and late August) and 7 out of 10 dates in 2007 (all except late May, late July, and late August) and significantly lower than Control treatment in early November 2006 (Fig. 3.6, Appendix F). The Girdle + Removal treatment soil temperature was significantly greater than the Girdle Only treatment in 8 out of 13 dates in 2006 (all except late April, late August, late September, early October, and early November) and 9 out of 10 dates in 2007 (all except late April). The Girdle Only treatment soil temperature was significantly greater than the Control treatment in 3 out of 13 dates in 2006 (mid May, late July, and mid August) and 3 out of 10 dates in 2007 (late May, late August, and early September) (Appendix F).

Soil moisture was affected by time and treatment*cover interaction. In 2006, soil moisture was greater in spring and fall yet dipped lower in summer, especially in mid June and August (Fig. 3.7a). In 2007, soil moisture was greater in spring and late summer than early summer and fall (Fig 3.7b). Volumetric soil water content averaged between 15.0 and 31.3 % in 2006 and 16.1 and 29.5 % in 2007 by treatment only and ranged from 11.2 to 37.2 % in 2006 and 13.3 and 35.4 % in 2007 when cover was also considered (Figs. 3.7, 3.8 and 3.9). Soil moisture tended to be greater in Control than Girdle Only, while Girdle + Removal soil moisture was in between the other treatments (Fig. 3.7). When cover was considered in addition to treatment, all treatments with *R. maximum* cover and Girdle Oak samples tended to have less soil moisture than Other cover in both 2006 and 2007 (Figs. 3.8 and 3.9). In 2006, both Control Oak and Girdle Other tended towards greater than average soil moisture while only Control Oak showed this trend in 2007. In 2006, Control Other, Girdle + Removal Oak, and Girdle + Removal Other had a tendency to have soil moisture fluctuate from about average to greater than average, while in 2007 Control Other, Girdle Other, Girdle + Removal Oak and Girdle + Removal Other tended to follow this trend..

Average soil respiration ranged from 1.9 to 6.5 μmol of CO_2 m^{-2} s^{-1} in 2006 and 2.7 to 11.9 μmol of CO_2 m^{-2} s^{-1} in 2007 (Fig. 3.10). While soil respiration was affected by time*treatment*cover interactions, there was not a consistent trend or pattern in soil respiration contributed by cover (Figs. 3.11 and 3.12). Soil respiration was significantly influenced by moisture and temperature. Average temperature-corrected soil respiration ranged from 1.9 to 6.6 μmol of CO_2 m^{-2} s^{-1} in 2006 and 2.7 to 11.8 μmol of CO_2 m^{-2} s^{-1} in 2007 (Fig. 3.13). While soil respiration was affected by time*treatment*cover interactions, there was not a consistent trend or pattern in soil respiration contributed by cover (Figs. 3.14 and 3.15).

The Girdle + Removal treatment significantly reduced soil respiration in 2006 and by August 2007 there was a distinct difference between the Girdle + Removal treatment and the other treatments. From mid July through early September 2007, soil respiration was almost half the value of the Control or Girdle Only treatment (Fig. 3.10). Soil respiration was significantly less in the Girdle + Removal treatment than Control 9 out of 13 dates in 2006 (all except mid May, early June, early July, and early November) and 9 out of 10 dates in 2007 (all except early May) (Fig. 3.10). When temperature-corrected, soil respiration was also significantly less in the Girdle + Removal treatment than Control in early May 2007 (Fig. 3.13). Soil respiration was significantly less in the Girdle + Removal treatment than the Girdle Only treatment on 4 out of 13 dates in 2006 (mid June, late July, mid August, late August) and 7 out of 10 dates in 2007 (all except late April, late May, and early July) (Fig. 3.10). When temperature-corrected, soil respiration was also significantly less in the Girdle + Removal Treatment than the Girdle Only Treatment in early July 2007 (Fig. 3.13). Soil respiration was significantly greater in the Girdle Only treatment than the Control on 1 out of 13 dates in 2006 (late August) and significantly less than the Control in 3 out of 10 dates in 2007 (late June, early July, and mid August) (Fig. 3.10).

DISCUSSION

The objective of this study was to quantify the effects of simulated SOD on aboveground litterfall and on soil temperature, moisture, and respiration under two possible scenarios. Previous studies at the Coweeta Hydrologic Laboratory have shown soil temperature, fine root mass, and litter quality were important regulating factors of soil CO_2 efflux (Vose et al. 1995, Bolstad and Vose 2005, Vose and Bolstad 2007). Loss of *Q. rubra* alone has the potential to change belowground dynamics via changes in litterfall quality and quantity, and the concomitant loss of *R. maximum* may lead to significant changes in carbon flux in southern Appalachian forests (Edwards and Harris 1977, Vose et al. 1995, Bolstad and Vose 2005, Vose and Bolstad 2007). The contribution of the two largest components of soil efflux, root biomass and microbial decomposition, are considered in addition to soil temperature and moisture, which are typically the most influential factors on rates of soil respiration (Edwards and Harris 1977, Vose et al. 1995, Bolstad and Vose 2005, Vose and Bolstad 2007).

Litterfall from September 2006 to March 2007 indicates that both treatments had the expected effects: greater litterfall in the Girdle Only treatment and a lack of *R. maximum* leaf litter in the Girdle + Removal treatment. Litter was greater in the Girdle Only treatment, which simulated an early stage of SOD with increased litter due to loss from dying *Q. rubra*, and litter was less in the Girdle + Removal treatment that simulated a later stage of SOD where litter input from both *Q. rubra* and *R. maximum* would decline. Total litterfall, and litter specifically from red oaks, *Rhododendron and Kalmia*, and other plant material (mostly woody twigs and branches) was greatest in the Girdle Only treatment where only the red oaks were girdled and *R. maximum* was left intact (Fig 3.1). This suggests a quick initial increase in litter due to the Girdle Only treatment, as previously observed in studies of girdling in *P. elliotii* and *T. canadensis* (Schroeer et al. 1999, Nuckolls et al. In Press). In the Girdle + Removal treatment, *Rhododendron* and *Kalmia* litter inputs were negligible (as expected due to the removal of *R. maximum)*, the proportion of other plant material was lower, and there was less total litter than in the Girdle Only treatment or the Control (Figs. 3.1 & 3.2).

Mean growing season CO_2 efflux ranged from 4.5-6.3 μmol m^{-2} s^{-1}, similar to other studies in the southern Appalachian forests which ranged from 5.6-8.15 μmol m^{-2} s^{-1} (Vose et al. 1995, Bolstad and Vose 2005, Vose and Bolstad 2007, Nuckolls et al. In Press). As hypothesized, results from the first two years post-treatment confirmed an immediate decrease in soil respiration in the Girdle + Removal treatment and no significant effect in the Girdle Only treatment. This contrasts with a previous study of the potential effects of HWA which found girdled Eastern hemlock reduced soil CO_2 efflux within the first two years after treatment (Nuckolls et al. In Press). Lower soil respiration in the Girdle + Removal treatment may be due to aboveground litter loss, as a previous study at Coweeta has shown litter exclusion can reduce soil respiration (Reynolds and Hunter 2001).

Girdling cuts off photosynthate supply that directly controls root respiration, so we expect girdled plots to have lower soil respiration. However, in the Girdle Only treatment, due to gradual mortality of *Q. rubra* and because belowground gaps created by girdling *Q. rubra* are expected to be less extensive and ephemeral compared to the extent and severity of belowground gaps created by *R. maximum* removal, we did not expect to see these effects during this intial study. Belowground root gaps were not detected in a previous study of girdling in slash pine (*Pinus elliotii* Engelm.) due to the rapid response of understory ground cover (Schroeer et al. 1999). Lower soil respiration only in the Girdle + Removal treatment suggests *R. maximum* removal created large, persistent belowground gaps, indicative of a net decrease in soil respiration, likely due to root death, rather than an increase in soil respiration due to increased microbial decomposition from greater input of dead root litter and increased temperature.

Soil temperature and moisture are typically the most influential factors on soil respiration rates, which are also influenced by root biomass, soil organic matter, litter quality, and soil and root N concentrations (Edwards and Harris 1977, Vose et al. 1995). As expected, soil temperature was slightly greater in the Girdle + Removal treatment than the Control or Girdle Only treatment due to increased light reaching the forest floor; however soil moisture did not decrease and was similar to Control in both the Girdle + Removal and Girdle Only treatments. In this study, average soil respiration was significantly affected by soil moisture and soil temperature.

Until recently, the accepted viewpoint was that soil activity is dominated by decomposer organisms processing detritus and that root litter inputs approximated aboveground litter (Högberg and Read 2006). Högberg and Read argue that evidence increasingly indicates that half of soil respiration is due to living plant roots, their mycorrhizal fungi and other root-associated microbes, and that this release is driven directly by recent photosynthesis (2006). The significant decrease in soil respiration in the Girdle + Removal treatment suggests that the increase in microbial decomposition due to greater availability of fine and coarse root litter and increased temperature did not outweigh the decrease in respiration attributed to the loss of aboveground litterfall and belowground roots, in addition to their mycorrhizal fungi and exudate-dependent root-associated microbes.

During the first few years after the loss of *Q. rubra* alone, numerous small gaps would open in the forest canopy as opposed to large gaps created by the loss of both *Q. rubra* and *R. maximum*. Due to the extensive understory cover provided by dense stands of *R. maximum*, *g*aps created by the loss of both *Q.rubra* and *R. maximum* are larger than gaps created by *Q. rubra* alone. Decades after the loss of *Q. rubra* alone, *R. maximum* would expand into gaps not filled by the increase in BA by trees that remain after SOD (i.e. those not suffering mortality or decline which make up a significant portion of current BA) (Clinton et al. 1994, Beckage et al. 2000, Chapter 2, Appendices A and B). In the case of loss of *Q. rubra* and *R. maximum,* in addition to the increase in basal area by trees that remain after SOD, *A. rubrum* is expected to dominate recruitment in gaps (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000, Chapter 2, Appendices A and B). As other hardwood species such as *A. rubrum* replace *R. maximum* and *Q. rubra*, changes belowground will, in turn, reinforce changes in community composition and ecosystem processes.

In both scenarios, dying and dead *Q. rubra* trees would contribute a pulse of low quality, high lignin:N and C:N litter and in the high severity scenario the amount of this litter would be even greater due to the loss of *R. maximum* shrubs (Coleman et al. 2004a, Monk et al 1985, Wardle 2002). The first few years after SOD, soil would continue to have a low pH, a significant proportion of organic N, and a slow C pool with a low rate of decomposition in both scenarios. Decades after SOD, soil will have a low pH, a significant proportion of organic N, and a slow C pool with a low rate of decomposition in the moderate severity scenario (Wardle 2002). Conversely, in the high severity scenario, soil pH and inorganic N (available to non-ericoid species) will increase and the C pool will be faster with an increased rate of decomposition (Wardle 2002). The replacement of recalcitrant, high lignin:N rhododendron and red oak litter by higher quality hardwood (i.e. red maple) litter should increase soil pH, N availability, and labile soil C (Wardle 2002).

While Vose and Bolstad (2007) observed considerable temporal variation in abiotic and biotic variables within and among forests of different age, only indices of litter and root quality correlated with forest floor CO_2 efflux. They suggest that differences in biotic variables correlated with forest floor CO_2 efflux among different age forests may have been related to shifts in the relative importance of heterotrophic and autotrophic respiration components to overall forest floor CO_2 efflux (Vose and Bolstad 2007). In the less severe scenario, litter quality is predicted to continue to be relatively low and ericoid mycorrhizae would increase dominance in proportion to the increase in *R. maximum* (Wurzberger and Hendrick 2007, Wardle 2002). In the worst-case scenario, the shift towards higher quality litter associated with *A. rubrum* would lead to a change in the soil microbial community, which would move from a recalcitrant system dominated by mycorrhizae to more fertile system with higher productivity, greater rates of decomposition, and an overall faster carbon cycle with a microbial assemblage containing arbuscular mycorrhizal associates of *A. rubrum* and bacteria, which prefer higher quality litter (Wardle 2002).

R. maximum inhibits recruitment of tree seedlings by restricting light and nutrient availability on the forest floor beneath it (Nilsen et al. 2001, Beier et al. 2005, Wurzberger and Hendrick 2007). Even after removal of overstory canopy, thickets of R. maximum inhibit the growth of woody seedlings (Clinton et al. 1994, Beckage et al. 2000). A recent study of suppression of oak seedlings shaded by *R. maximum* found that photosynthesis was reduced and seedlings were limited by carbohydrate availability, which in turn limited their capacity to produce defensive compounds, making them more susceptible to herbivory (Beier et al. 2005).

"Hoarding" of nitrogen via organic complexes, more so than light limitation, is thought to lead to the suppression of seedling regeneration underneath rhododendron and lower diversity in the forest (Wurzberger and Hendrick 2007). *R. maximum* alters N cycling through the formation of polyphenol–organic N complexes, which create a recalcitrant litter that is subsequently processed by mutualistic ericoid mycorrhizae via special enzymes (Wurzberger and Hendrick 2007). Non-Ericaceous plant species do not have access to ericoid mycorrhizae and their enzymes and rely on inorganic N for their nutrition. If other Ericaceous species present in this system, such as *Rhododendron calendulaceum*, *Kalmia latifolia*, *Vaccinium corymbosum* and *Gaylussacia ursina*, are resistant to *P. ramorum* or less severely affected by SOD they likely have an advantage over non-Ericaceous species in competing for nutrients in gaps created by loss of *R. maximum.* The future forest may be dominated by understory thickets of huckleberry (*G. ursina*, which due to their current abundance are poised spread into gaps) and an overstory canopy of red maple.

While SOD infection has been detected in nurseries in the southeastern U.S., the USDA Forest Service Sudden Oak Death National Detection Survey has not found SOD in forests adjacent to nurseries, general forest transects, or in stream baiting in the southern Appalachians (Stokstad 2004, Oak et al. 2007). Forest professionals who notice the tell-tale signs of cankers and leaf blight should quickly contact local authorities (USDA Forest Service, USDA Animal and Plant Health Inspection Service, or other local plant pathogen specialists) to test suspect plants. Any initial outbreak will need to be contained by following established guidelines to prevent its spread, such as removal and burning of infected plants as has been practiced in Oregon (Goheen et al. 2002). Short-term impacts (e.g. oak cankers and *R. maximum* foliar infection) of the disease will be apparent within a few years of infection, while longer-term effects will arise from the gradual mortality of individual trees and the successive establishment and growth of a new species mix. We do not know how severe or widespread the effects of SOD in the southern Appalachians will be and therefore must prepare contingencies for a number of different scenarios.

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TABLES

Table 3.1 Calendar of field measurements and experimental treatment.

	Summer 2005	Fall 2005	Winter 2005-6	Spring 2006	Summer 2006	Fall 2006	Spring 2007	Summer 2007	Fall 2007
Tree and shrub survey	X								
Understory richness & cover	X			X	X		X	X	X
Understory seedling count		X				X	X	X	X
Canopy light interception		X							
Girdling and *R. max* removal			X						

Table 3.2 Pre-treatment basal area and density by treatment. *Q. rubra* and *R. maximum* are listed separately in addition to totals for each treatment block.

		Basal Area (m^2ha^{-1})						Number of stems ha^{-1}					
Treatment		Total (SD)		Trees (SD)		Shrubs (SD)		Total (SD)		Trees (SD)		Shrubs (SD)	
Control		40.2	(7.5)	35.0	(4.1)	5.2	(3.4)	5737	(1857)	619	(293)	5119	(1564)
	Q. rubra	10.1	(2.9)	10.1	(2.9)	0.0	(0.0)	126	(55)	85	(13)	41	(61)
	R. max	4.9	(5.6)	1.8	(2.7)	3.1	(2.9)	1856	(930)	148	(219)	1707	(745)
Girdle		35.1	(13.0)	31.8	(11.2)	3.3	(1.9)	3807	(1201)	348	(61)	3459	(1240)
	Q. rubra	9.6	(3.0)	9.5	(2.9)	0.0	(0.1)	63	(45)	56	(33)	7	(13)
	R. max	2.5	(0.5)	0.3	(0.6)	2.1	(0.7)	1804	(246)	33	(58)	1770	(230)
Girdle + Removal		34.6	(10.4)	31.4	(9.9)	3.2	(0.7)	3630	(1161)	356	(88)	3274	(1104)
	Q. rubra	13.3	(6.6)	13.3	(6.6)	0.0	(0.0)	70	(39)	67	(40)	4	(6)
	R. max	2.1	(0.1)	0.3	(0.3)	1.7	(0.4)	1452	(265)	30	(28)	1422	(290)

FIGURES

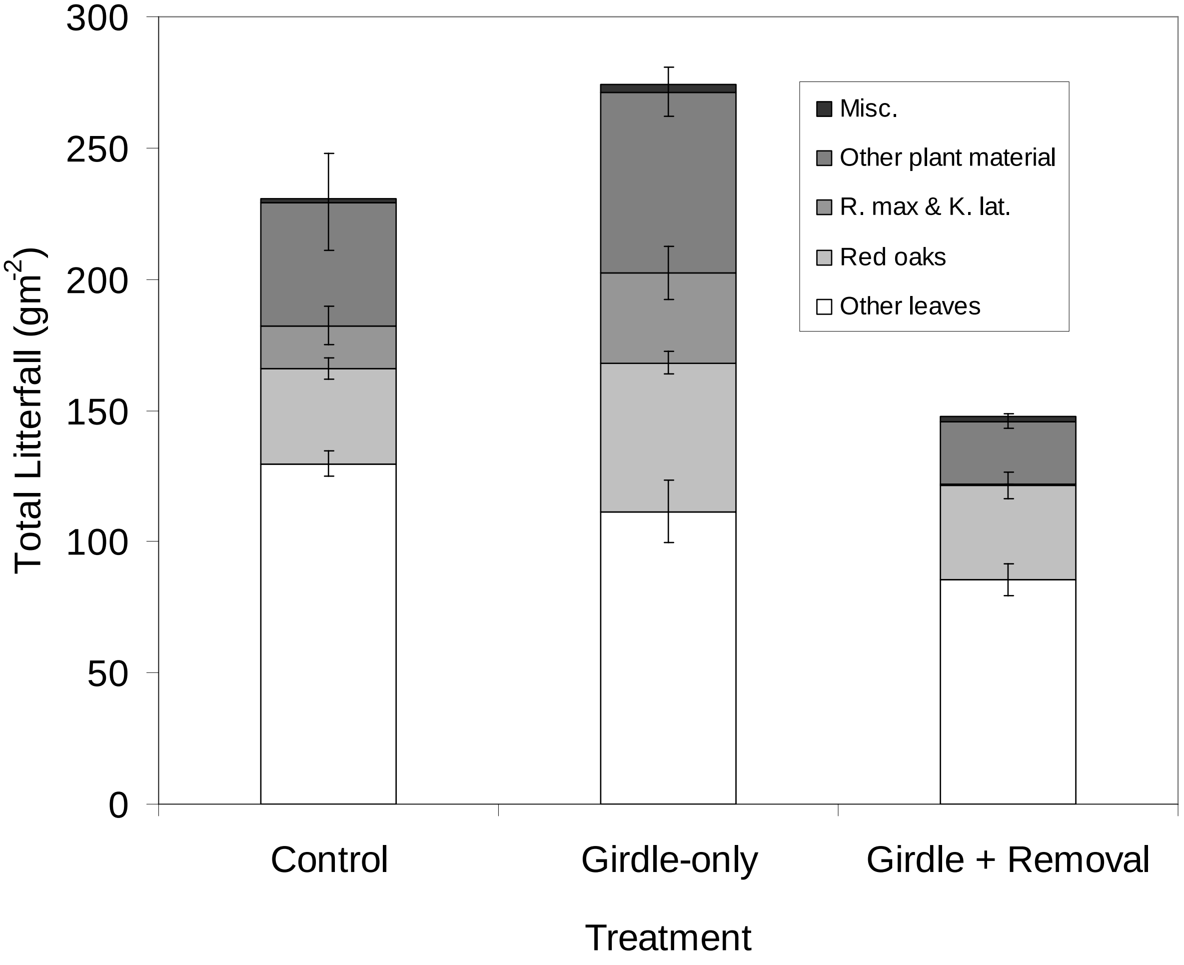


Figure 3.1 Total litterfall collected between September 2006 and March 2007. Listed by treatment and litter type.

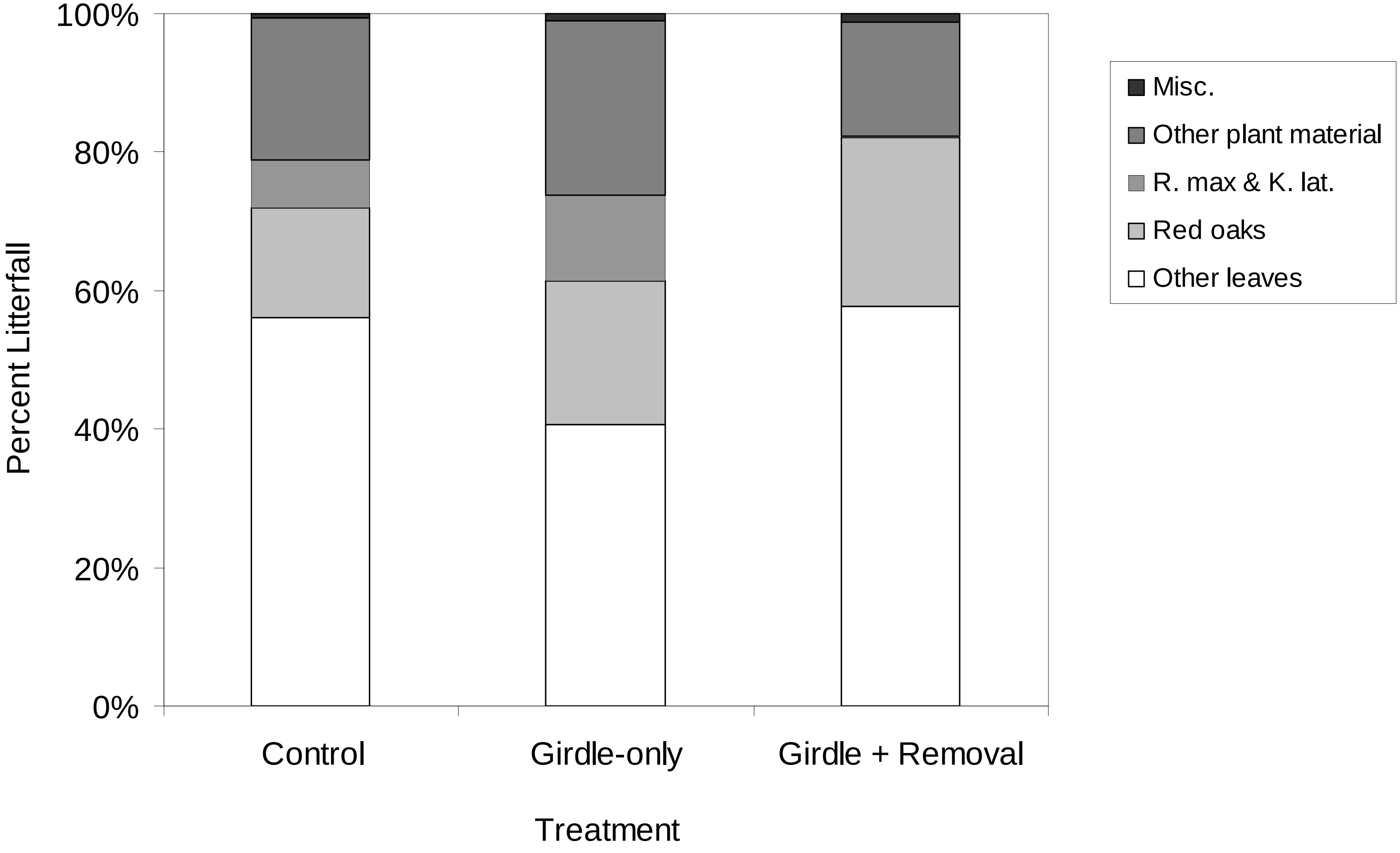


Figure 3.2. Percent litterfall collected between September 2006 and March 2007. Listed by treatment and litter type.

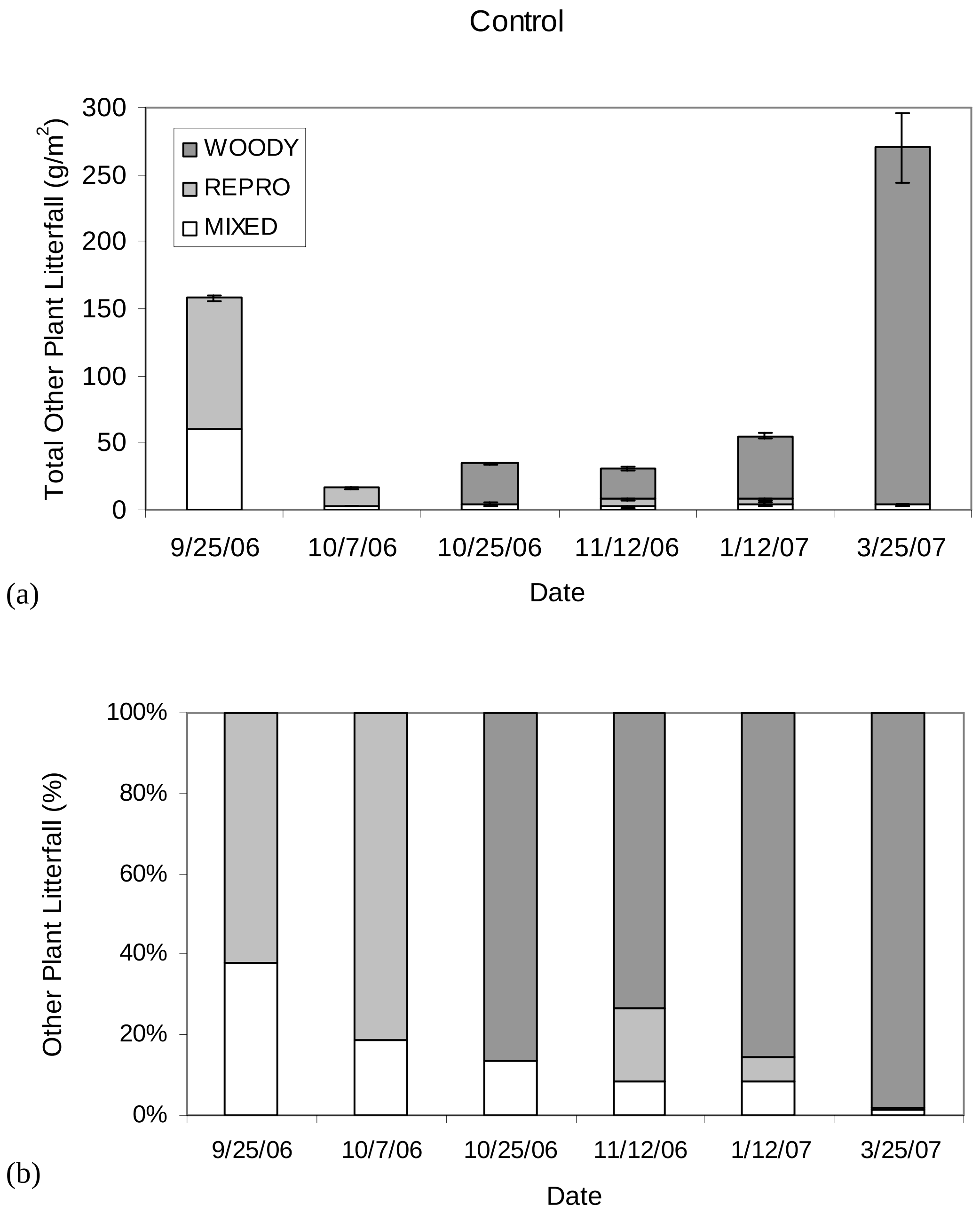


Figure 3.3 Estimated contribution of woody and reproductive litter in the control treatment. Listed by (a) total amount and (b) percent of total other plant material for each collection date.

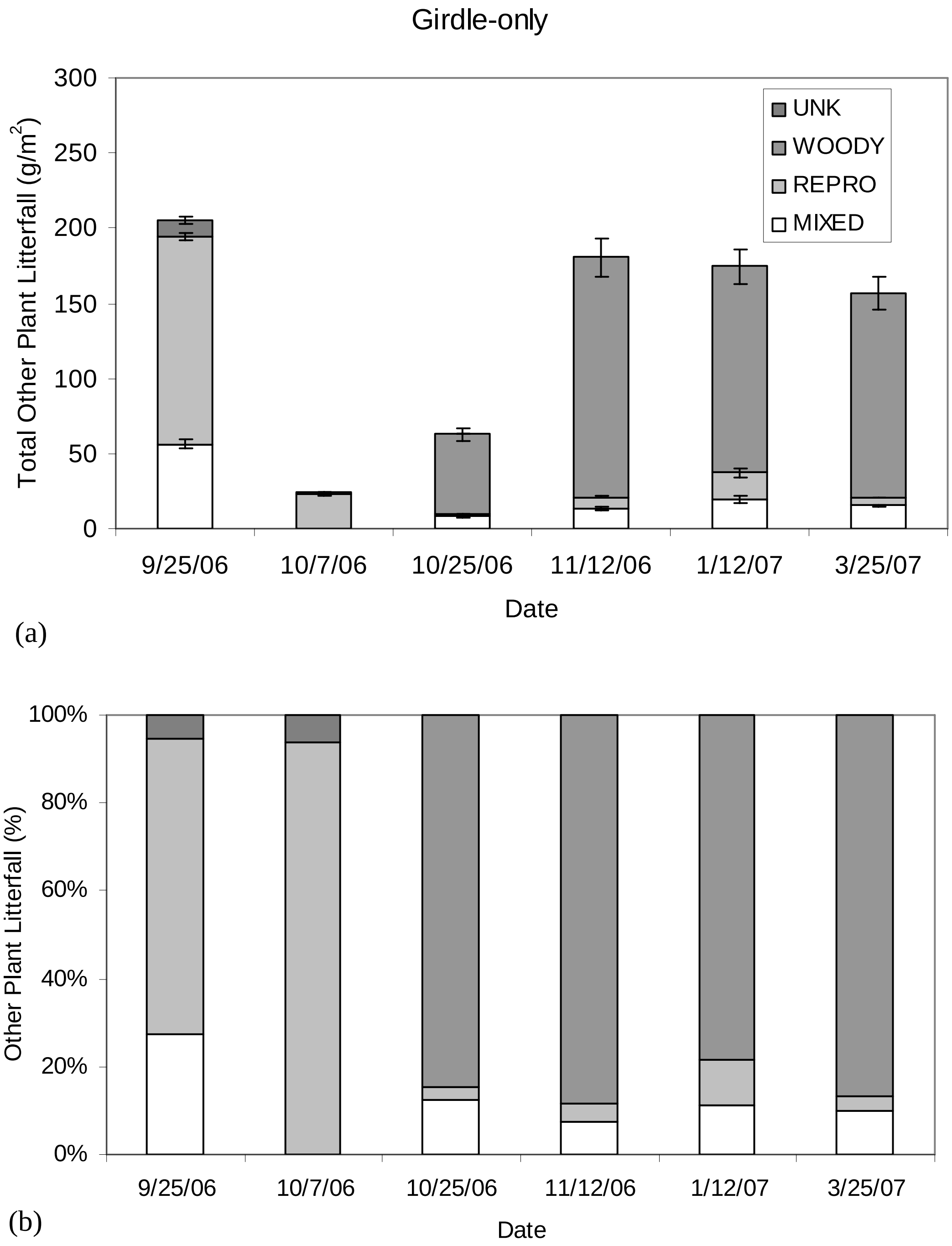
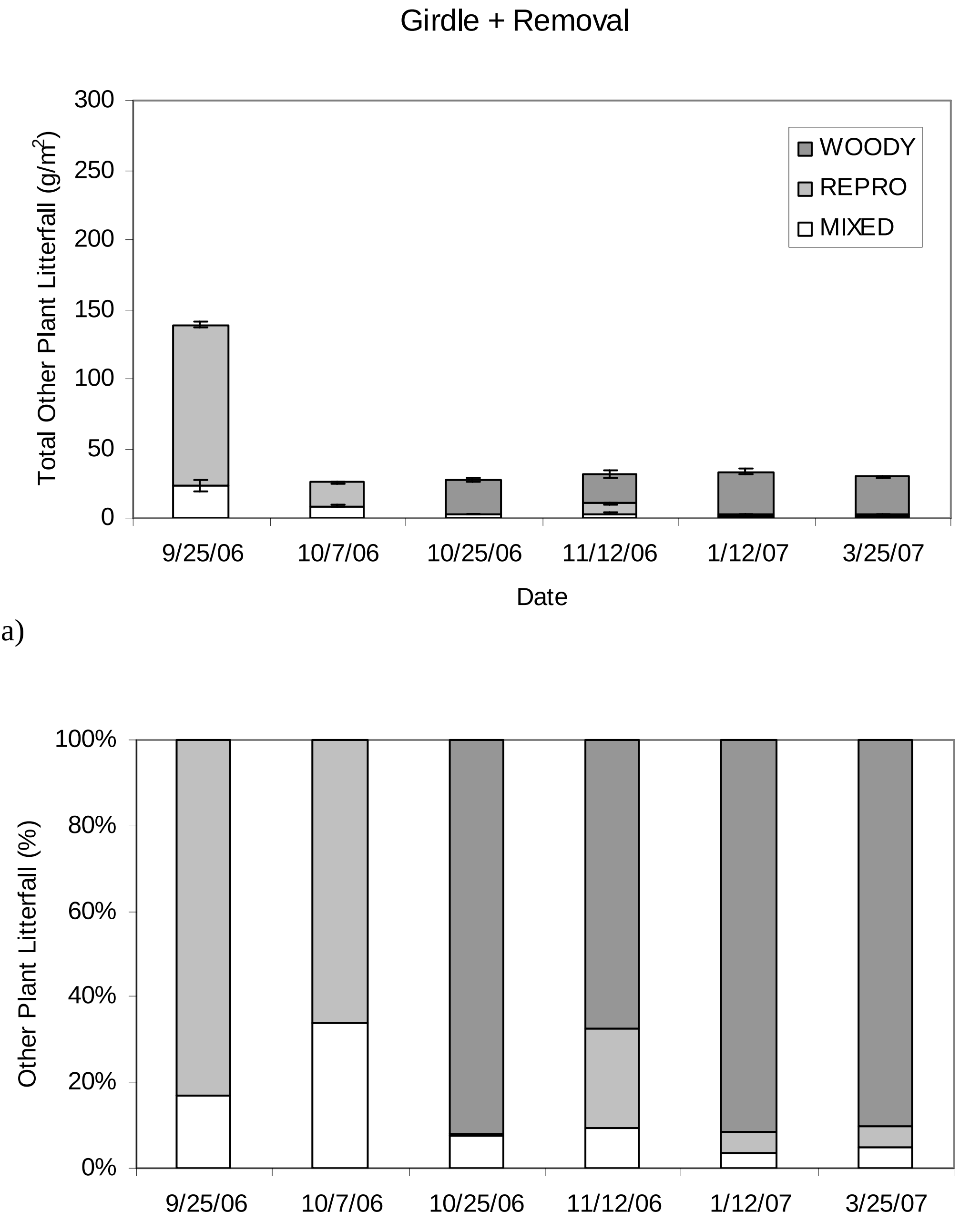


Figure 3.4 Estimated contribution of woody and reproductive litter in the Girdle Only treatment. Listed by (a) total amount and (b) percent of total other plant material for each collection date.



(a)

(b)

Figure 3.5 Estimated contribution of woody and reproductive litter in the Girdle + Removal treatment. Listed by (a) total amount and (b) percent of total other plant material for each collection date.

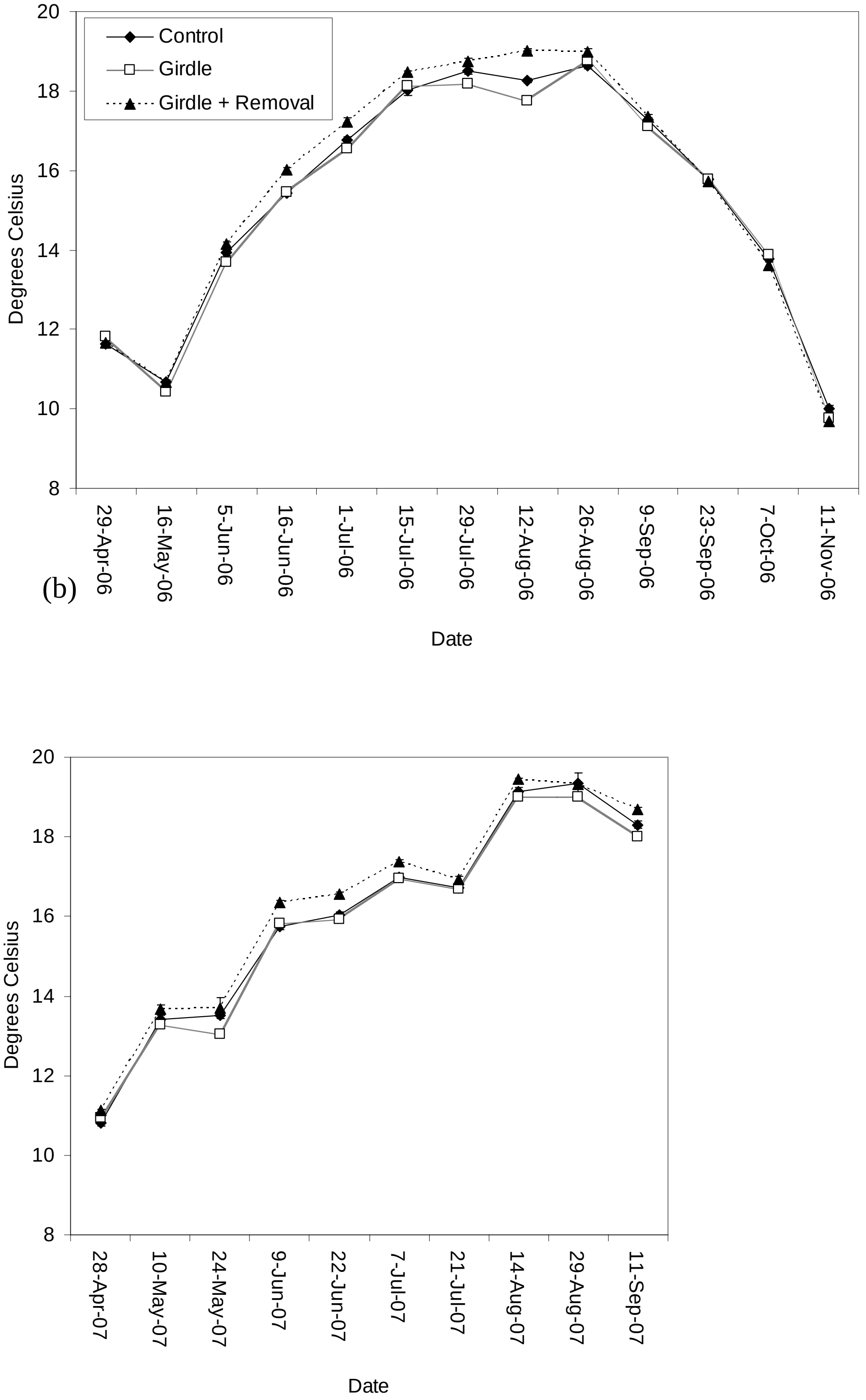


Figure 3.6 Average soil temperature across the growing season. (a) 2006. (b) 2007.

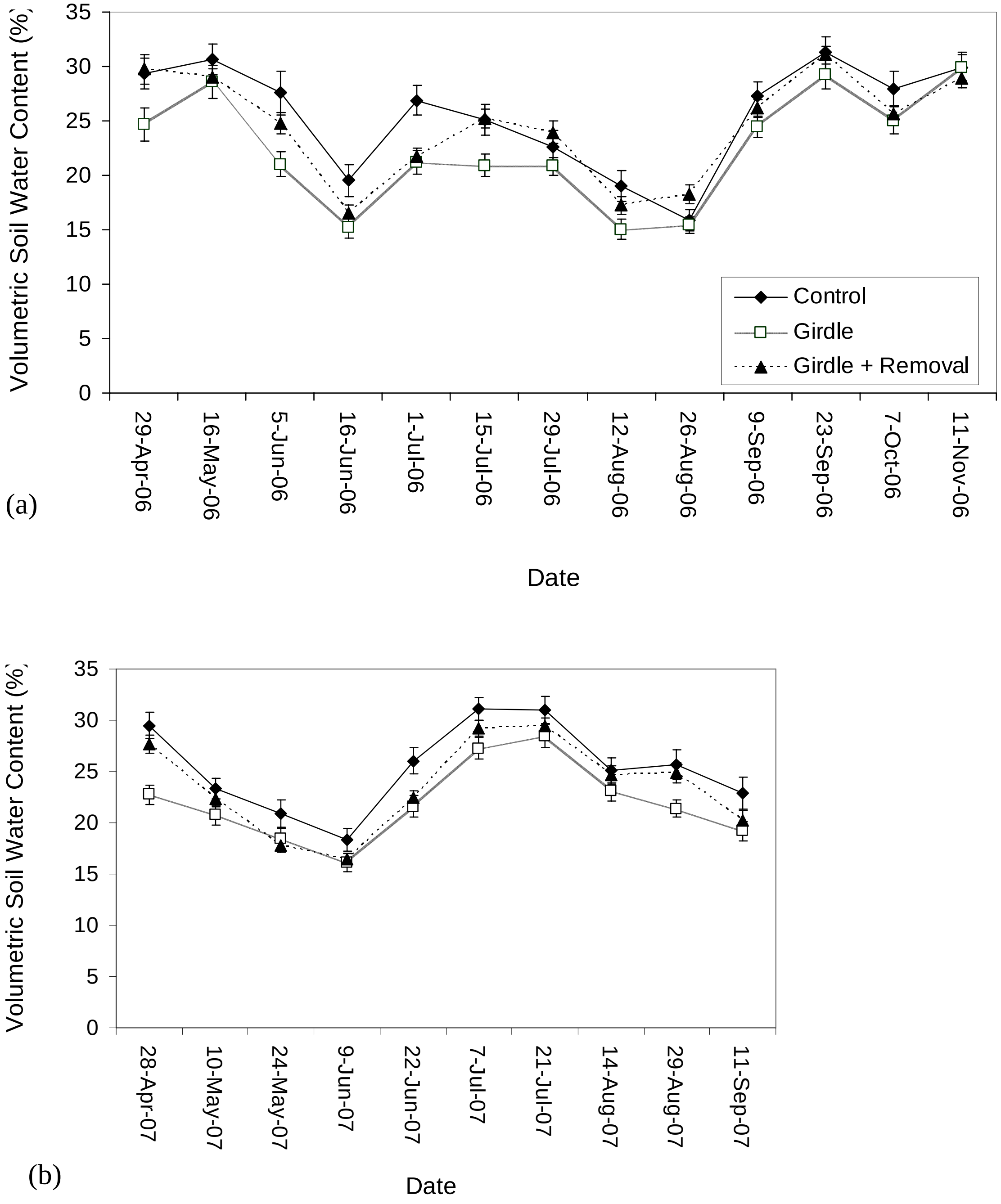


Figure 3.7 Average soil moisture across the growing season. (a) 2006. (b) 2007.

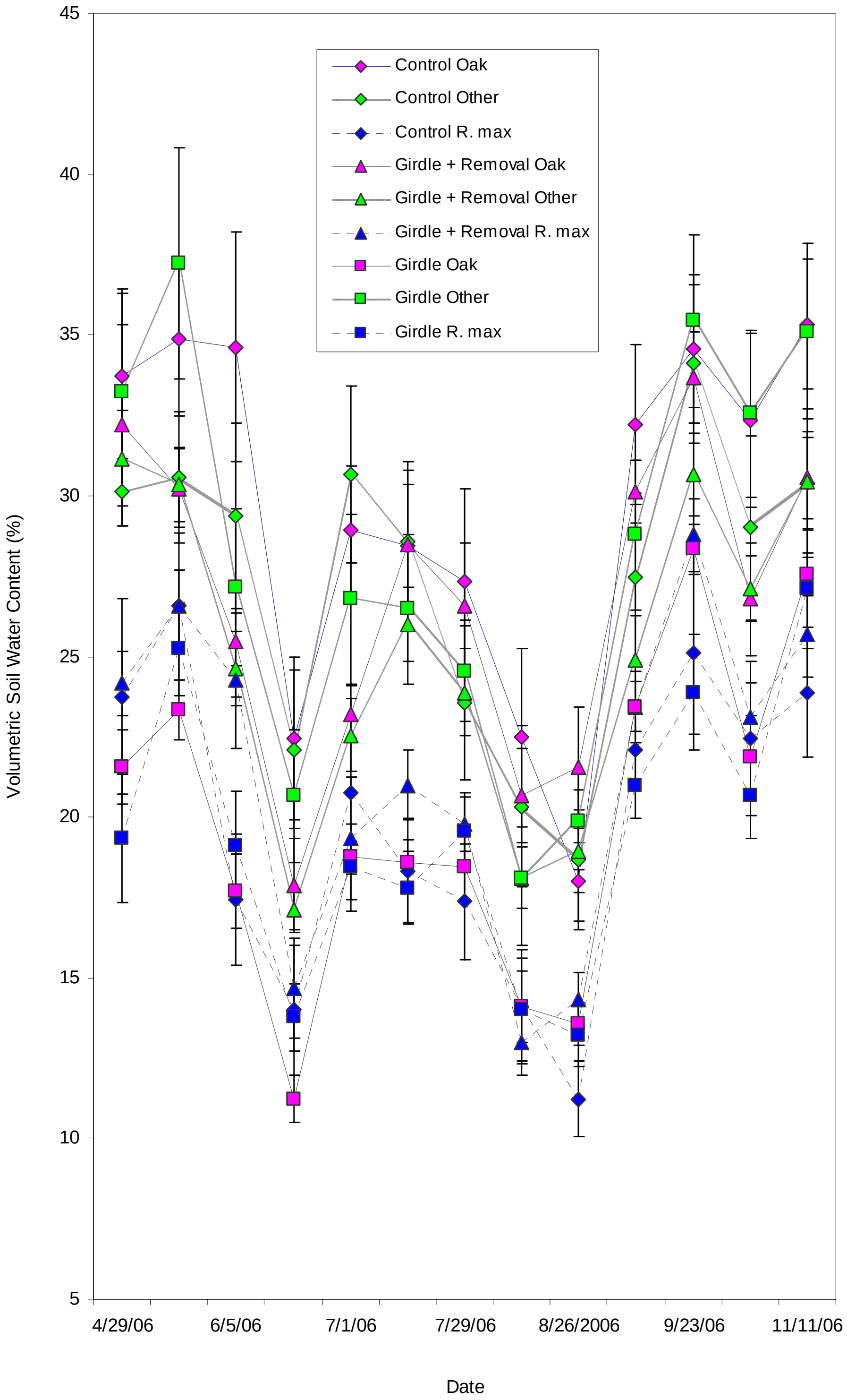


Figure 3.8 Average soil moisture by treatment and aboveground cover across the growing season for 2006.

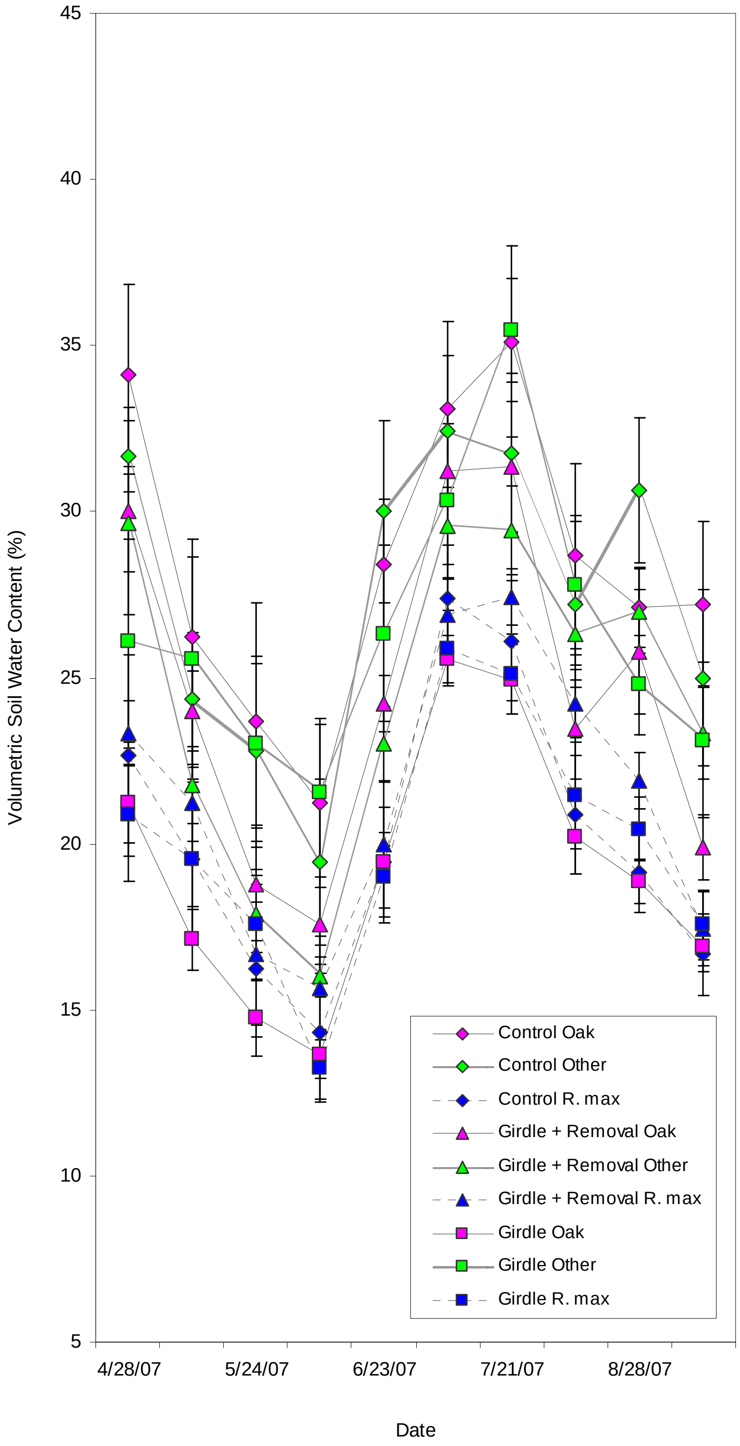


Figure 3.9 Average soil moisture by treatment and aboveground cover across the growing season for 2007.

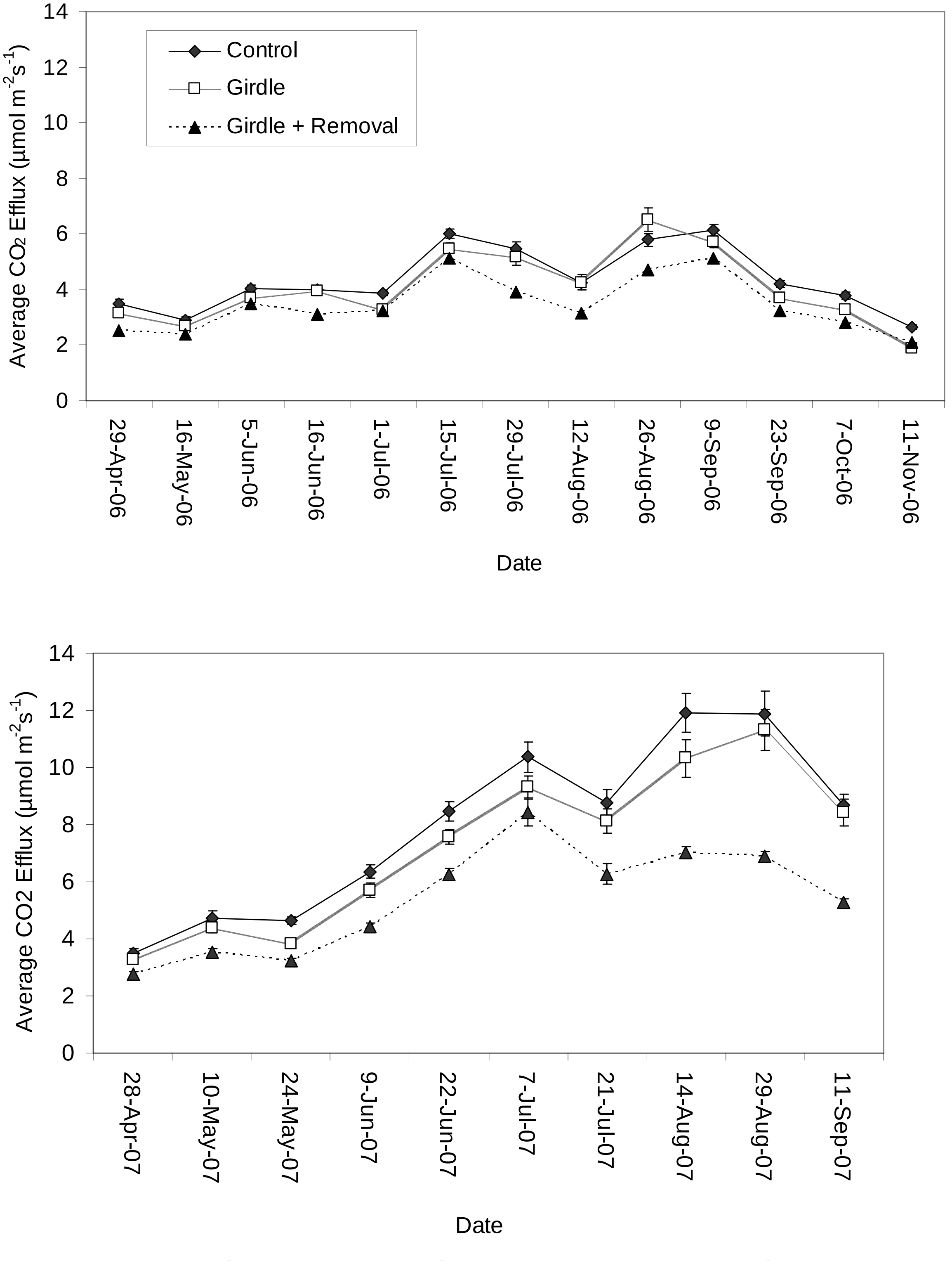


Figure 3.10 Average soil respiration across the growing season. (a) 2006. (b) 2007.

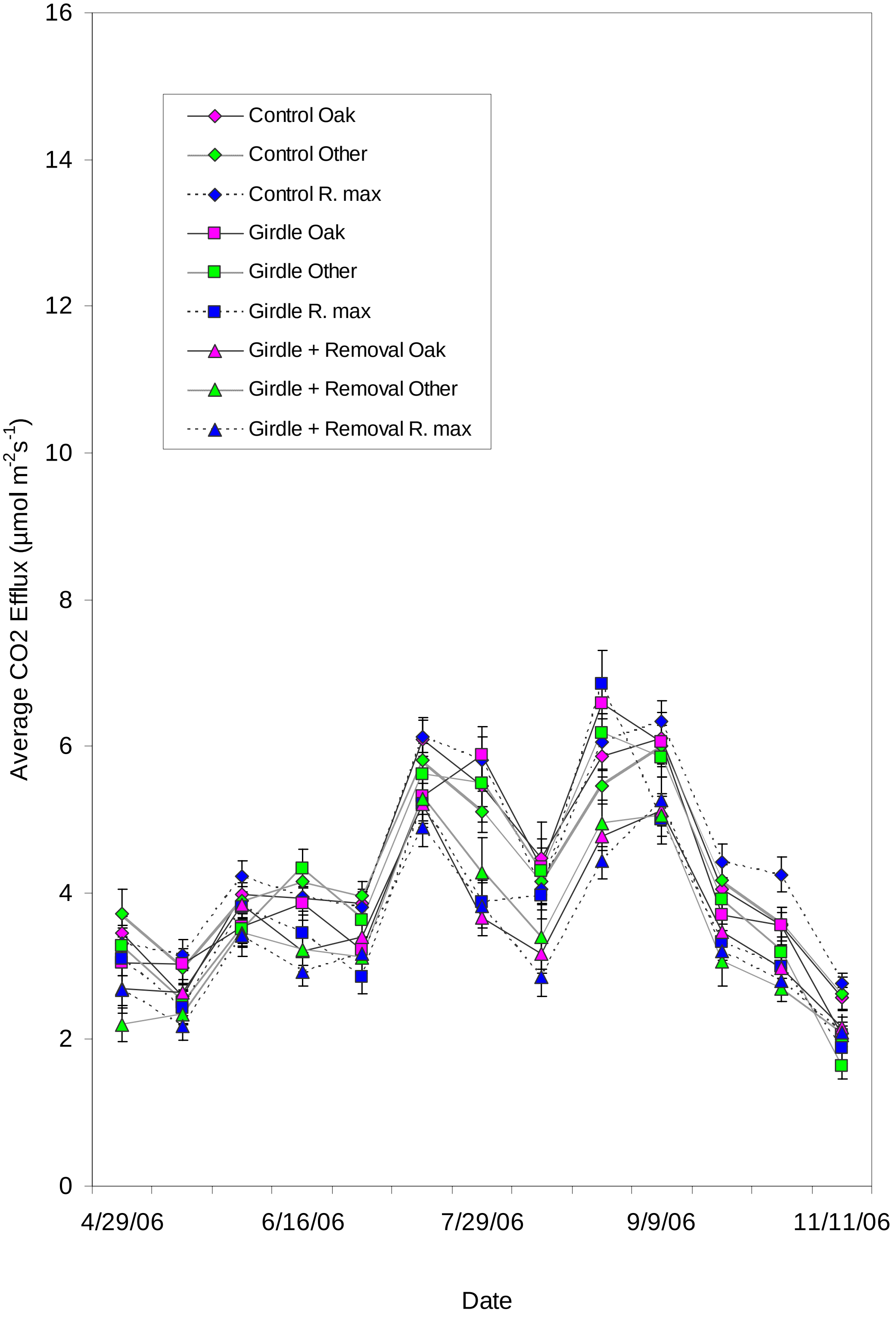


Figure 3.11 Average soil respiration by treatment and aboveground cover across the growing season for 2006.

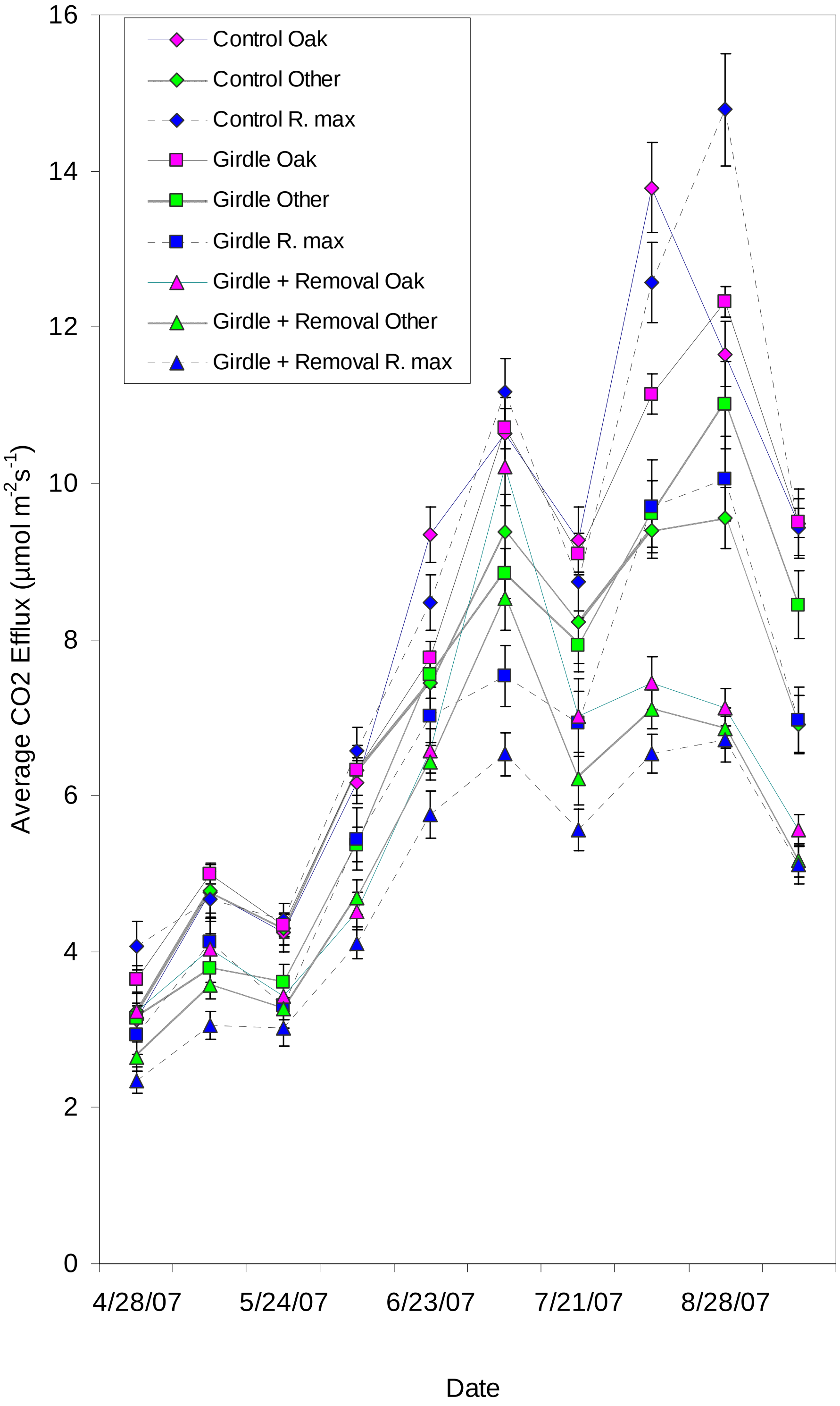
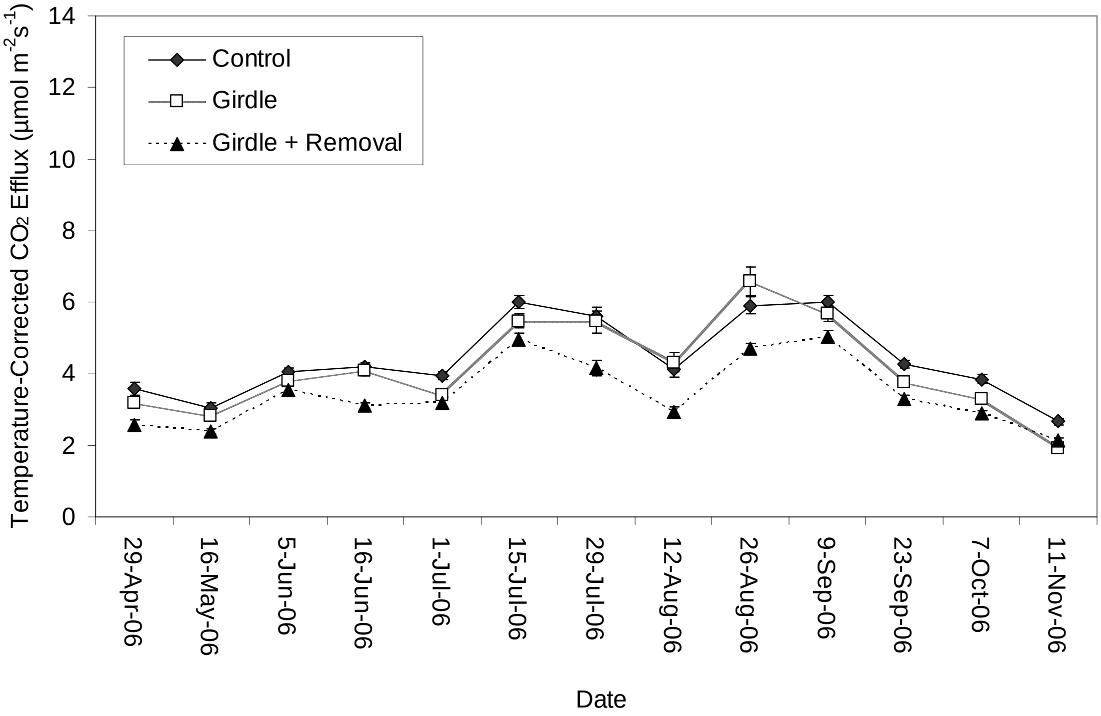
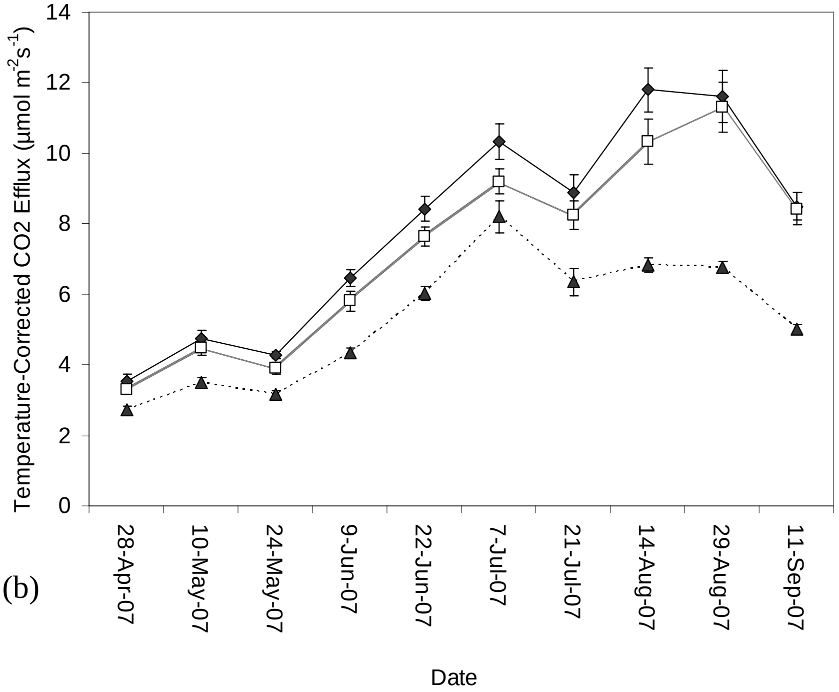


Figure 3.12 Average soil respiration by treatment and aboveground cover across the growing season for 2007.



(a)



(b)

Figure 3.13 Average termperature-corrected soil respiration across the growing season. (a) 2006. (b) 2007.

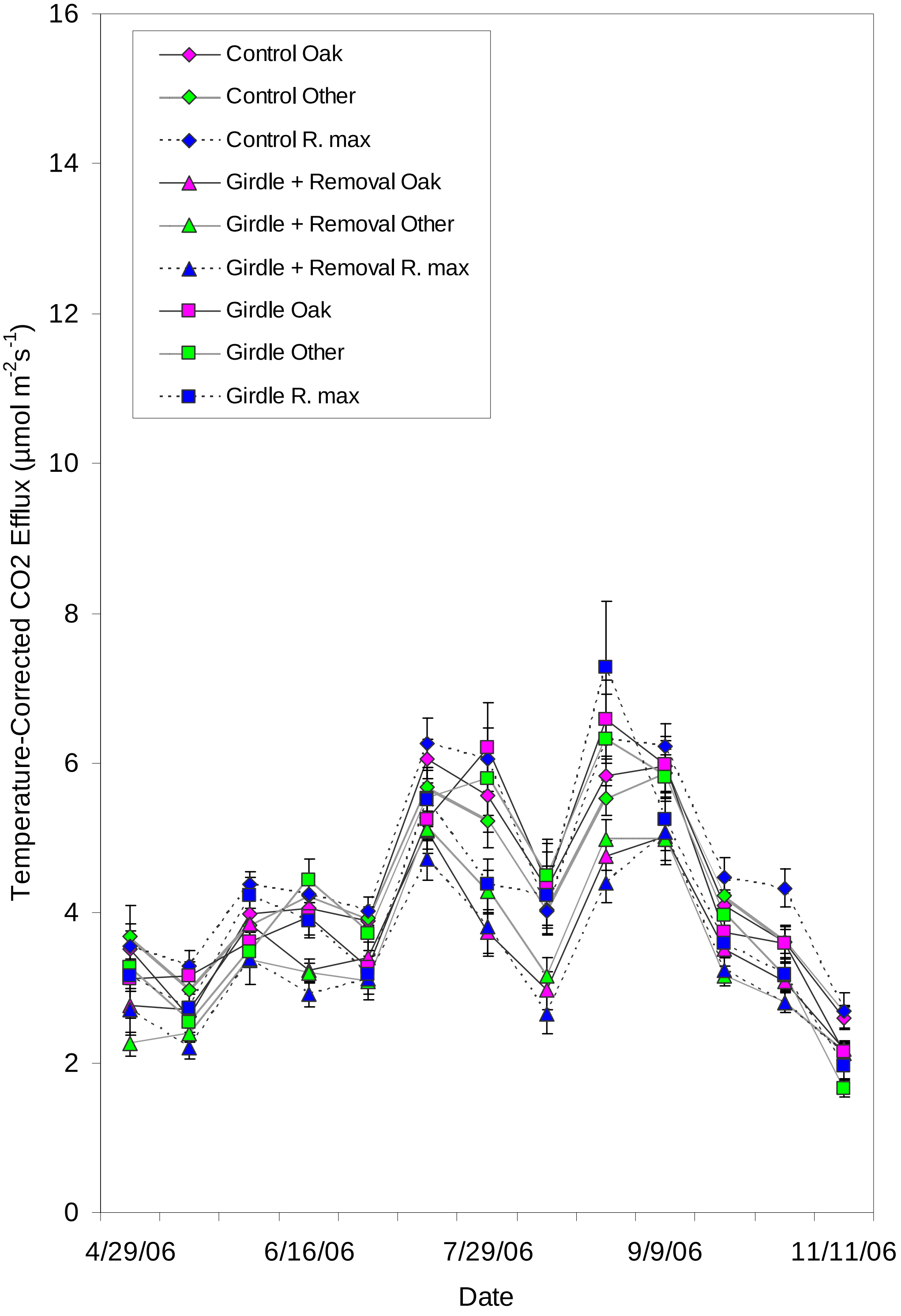


Figure 3.14 Average temperature-corrected soil respiration by treatment and aboveground cover across the growing season for 2006.

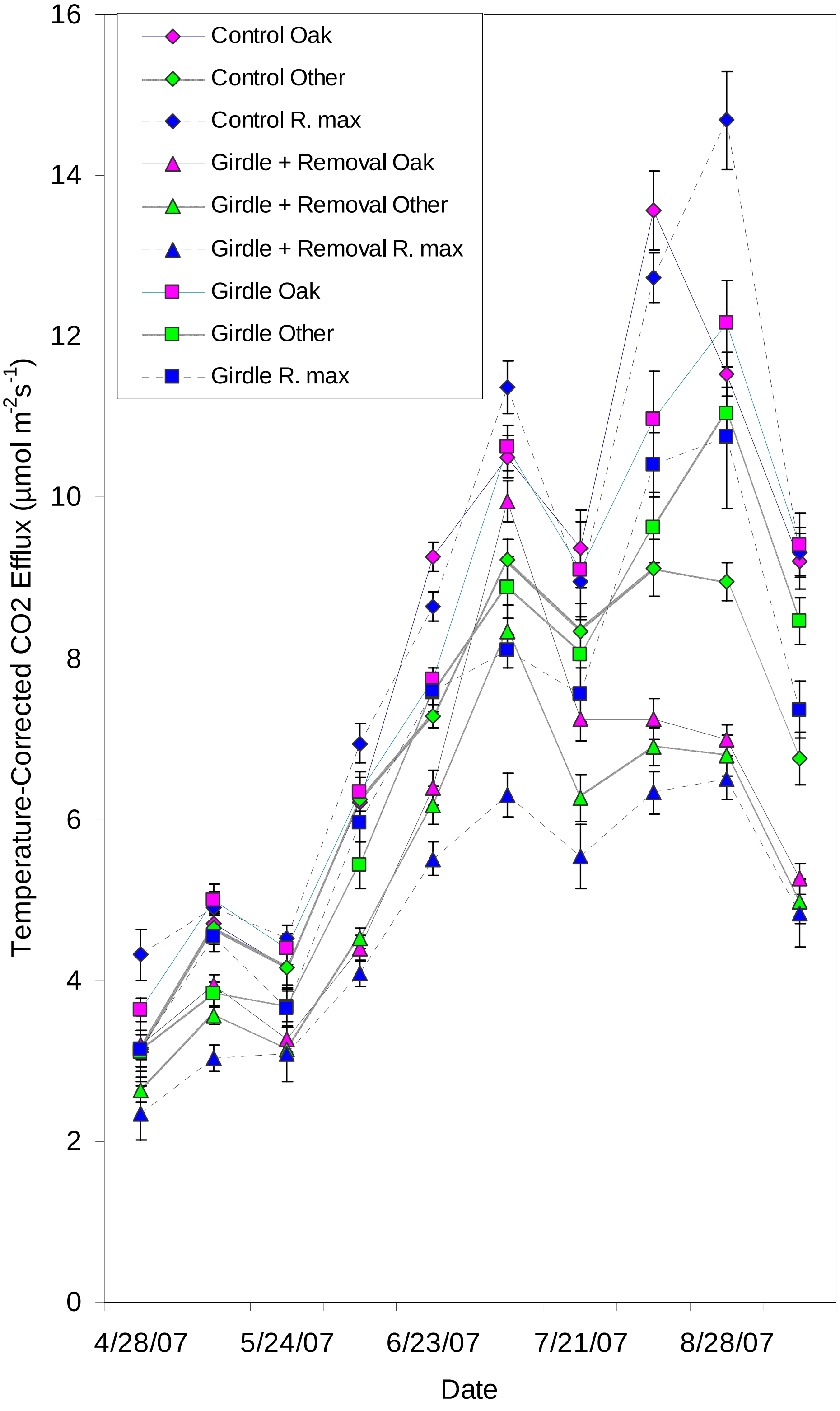


Figure 3.15 Average temperature-corrected soil respiration by treatment and aboveground cover across the growing season for 2007.

CHAPTER 4

SUMMARY AND CONCLUSION

This study quantified the effects of simulated SOD under two possible scenarios. Under the first scenario, *Q. rubra* were girdled to simulate a moderate severity SOD outbreak with high mortality of red oaks only. The high-severity scenario treatment, with red oaks girdled and *R. maximum* cut and removed from the site, simulated the loss of both red oaks and rhododendron, with the concomitant loss of aboveground biomass and litter input.

In chapter 2, I addressed potential aboveground effects of SOD on understory vegetation and seedling establishment. I presented analyses of herbaceous layer species richness, community similarity, and percent cover and reported woody seedling density, abundance, and species composition. Results from the first two years post-treatment demonstrate subtle changes in understory vegetation and seedling establishment in the moderate severity treatment and more pronounced changes in .the high severity treatment. Woody species richness and seedling density increased in the high severity scenario. Summer estimates of similarity indicate that the plant community in southern Appalachian forests may change with either scenario of SOD. Chi-square analysis indicates that woody species composition differed among treatments under both scenarios, however, changes in fall may not be valid due to small sample size.

In chapter 3, I addressed potential belowground effects of SOD. In the first two years post-treatment, litterfall in both scenarios was as expected: due to aboveground loss of biomass there was more litterfall in the moderate severity treatment and less litter in the high severity treatment, which simulated a later stage of SOD when *R. maximum* litter would no longer be contributed. As expected, soil temperature was slightly greater in the high severity treatment than the control or moderate severity treatments; however soil moisture did not decrease and was similar to control in both scenarios. While there was no significant effect on soil respiration in the moderate severity scenario, lower soil respiration in the high severity scenario treatment suggests *R. maximum* removal created large, persistent belowground gaps, indicative of an overall decrease in root and microbial respiration rather than an increase in respiration due to greater litter input from dead roots and increased temperature. As other hardwood species such as red maple (*Acer rubrum*) replace *R. maximum* and *Q. rubra*, changes belowground will feed back aboveground to reinforce changes in community composition and ecosystem processes.

Current knowledge about southern Appalachian plant and soil ecology, SOD and conclusions from the plant and soil experiments can be combined to create a conceptual model of the potential effects of SOD in the Southern Appalachians (Figure 4.1). The forest prior to SOD contains the following dominant plant species and respective average basal area (based on experimental plots): *Q. rubra*: 30 %, *R. maximum*: 10 %, and *A. rubrum*, *Q. prinus*, and other hardwood species: 20 % each. The initial litter quality is relatively low, with a high ratio of lignin:N and C:N. Soil starts out dominated by ericoid and ecto-mycorrhizae (associates of *R. maximum* and *Q. rubra*, respectively) with a low pH, a significant proportion of organic N (due to complexing by ericoid mycorrhizae, Wurzburger and Hendrick 2007) and a slow C pool with a low rate of decomposition.

In the moderate severity scenario, Q. *rubra* would be removed from the forest. The first few years after loss of *Q. rubra* numerous small gaps would open in the forest where trees die. Dying and dead *Q. rubra* trees would contribute a pulse of low quality, high lignin:N and C:N litter (Coleman et al. 2004). Soil would continue to have a low pH, a significant proportion of organic N, and a slow C pool with a low rate of decomposition begin to be dominated by ericoid mycorrhizae. Decades after loss of Q. *rubra, R. maximum* would fill in most gaps (Clinton et al. 1994, Beckage et al. 2000). Litter quality would continue to be relatively low, with a high ratio of lignin:N and C:N (Wardle 2002). Soil would be dominated by ericoid mycorrhizae with a low pH, a significant proportion of organic N, and a slow C pool with a low rate of decomposition (Wardle 2002).

In the high severity scenario, Q. *rubra* and *R. maximum* would be removed from the forest. The first few years after loss of *Q. rubra* and *R. maximum* large gaps would open in the forest. Dying and dead *Q. rubra* trees and *R. maximum* shrubs would contribute a pulse of low quality, high lignin:N and C:N litter (Coleman et al. 2004, Monk et al 1985, Wardle 2002). Soil would continue to have a low pH, a significant proportion of organic N, and a slow C pool with a low rate of decomposition and begin to be dominated by ericoid and ecto-mycorrhizae (Wardle 2002). Decades after loss of Q. *rubra* and *R. maximum, A. rubrum* would fill in most canopy gaps (Clinton et al. 1994, Beckage et al. 2000). Litter quality would be relatively higher, with a lower ratio of lignin:N and C:N. Soil would be dominated by arbuscular mycorrhizae (associates of A. *rubrum*) and bacteria with a higher pH, inorganic N (more available to non-ericoid species), and a faster C pool with an increased rate of decomposition (Wardle 2002).

Other disturbance factors - wind, logging, urbanization, fire, and disease- will interact with SOD to determine the future plant community (Douglass and Hoover 1988). Climate change is predicted to alter temperature, precipitation patterns, and storm frequency and intensity and could lead to changes in the forest community composition as well as affecting the spread and pathogenicity of *P. ramorum* and other disturbances with which it interacts (Dale et al. 2001). In areas of the forest where hemlock is present, HWA may eliminate Eastern hemlock while SOD takes out oaks, Ericaceous species, and additional susceptible hardwoods. All of these factors need to be considered in planning for management of SOD.

For example, prescribed fire may be an option for SOD management in the Southern Appalachians. Areas in California burned since 1950 appear to have resistance to SOD, which is thought to be due to post-fire vegetation composition or soil chemicals unfavorable to *P. ramorum* (Moritz and Odion 2005). Results from a study of dogwood anthracnose, *Discula destructiva*, a fungal pathogen of flowering dogwood, *Cornus florida*, suggest that prescribed fire promotes forest structure and composition that is unfavorable to the disease (Holzmueller et al. 2008). Prescribed fire is being used in southern Appalachian forests to promote oak regeneration and suppress shade tolerant *A. rubrum*, the species most likely to replace lost oaks and R. maximum, and fire intolerant *R. maximum* plants, the predicted major host of *P. ramorum* (Clinton et al. 1994, Clinton and Vose 1996, and Beckage et al. 2000, Elliot et al. 1999). While prescribed fire may help control *R. maximum* and thus the major potential source of *P. ramorum* innoculum, *A. rubrum* - the species most likely to replace oaks and *R. maximum* lost to SOD- is also suppressed by fire, potentially complicating predictions of changes in the plant community. Prescribed fire may have the added benefit of killing *P. ramorum* spores in plants and soil.

This study will be continued under the Coweeta Long Term Ecological Research program in anticipation that in the long-term, species richness, percent cover, and woody seedling density may decrease, as red maple (*Acer rubrum*) successfully colonize and persist in gaps created by loss of *R. maximum* and *Q. rubra*. We expect that long-term, litterfall and soil temperature, moisture, and respiration will stabilize as existing plants and new seedlings colonize the belowground space left by *R. maximum* and *Q. rubra.* A concurrent study seeks to assess soil nutrients as a result of the same experiment. Data from these studies will be used to develop a predictive model of the effects of SOD in the southern Appalachians. Other related studies proposed include monitoring changes in soil fauna and soil food webs, effects on migratory birds or other wildlife, and potential effects on stream chemistry and biology. Future studies should consider the potential loss of Q. *prinus* and Q. *alba* in addition to *Q. rubra* and *R. maximum*. When this study began, the potential pathogenicity of *P*. ramorum on white oaks was not known, and these species were not manipulated in our experiment. However, a recent study on seedlings indicates that Q. *prinus* and Q. *alba* may be more susceptible, at least as seedlings, than Q. *rubra* (Tooley and Kyde 2007).

Changes in plant community structure and diversity due to disturbance have the potential to affect ecosystem production, decomposition, and nutrient cycling, which, in turn, determine plant species composition. The severity of SOD impact in the forest will depend on the timeframe of infection and progression of disease, the actual mortality of trees and shrubs, and the resistance and resilience of the plant community. Land managers will be faced with new challenges in trying to protect and restore desired plant species composition in the face of ecological changes arising from SOD. Short-term impacts (e.g. oak cankers and *R. maximum* foliar infection) of the disease will be apparent within a few years of infection, while longer-term effects will arise from the gradual mortality of individual trees and the successive establishment and growth of a new species mix. We do not know how severe or widespread the effects of SOD in the southern Appalachians will be and therefore must prepare contingencies for a number of different scenarios. While SOD infection has been detected in nurseries in the southeastern U.S., the USDA Forest Service Sudden Oak Death National Detection Survey has not found SOD in forests adjacent to nurseries, general forest transects, or in stream baiting in the southern Appalachians (Stokstad 2004, Oak et al. 2007). Forest professionals who notice the tell-tale signs of cankers and leaf blight should quickly contact local authorities (USDA Forest Service, USDA Animal and Plant Health Inspection Service, or other local plant pathogen specialists) to test suspect plants. Any initial outbreak will need to be contained by following established guidelines to prevent its spread, such as removal and burning of infected plants as has been practiced in Oregon (Goheen et al. 2002). Current and future monitoring to detect infection and collect data on ecological effects is essential to make appropriate management decisions.

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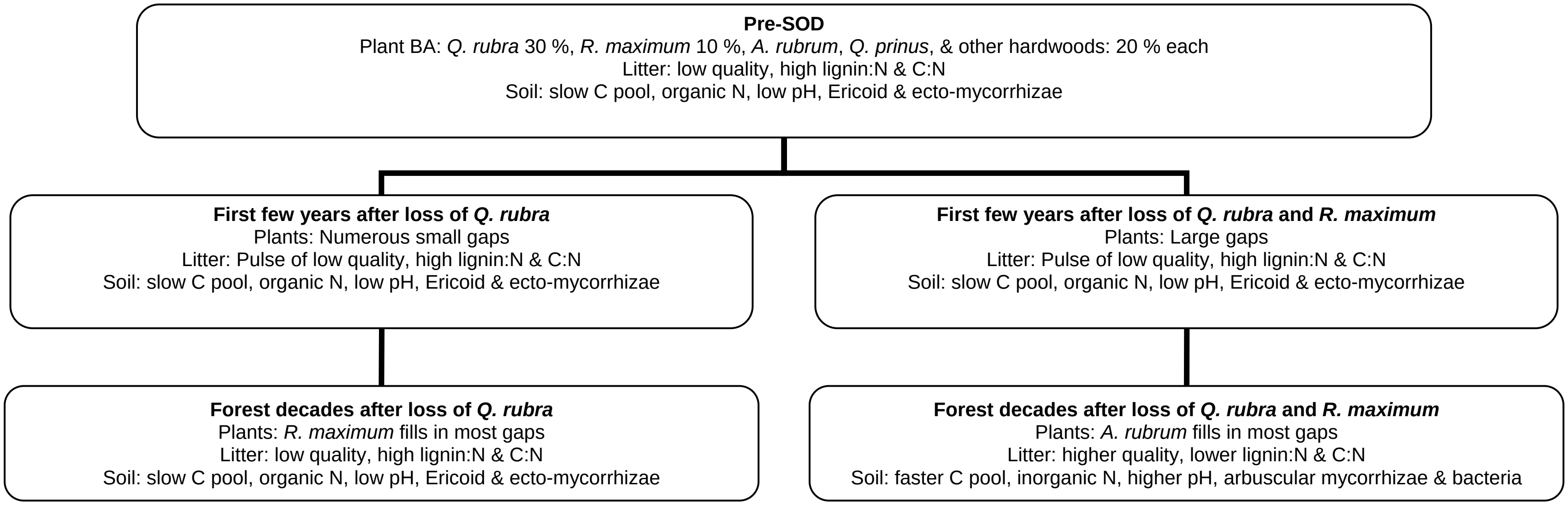

Figure 4.1 Conceptual model of SOD experimental scenarios.

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APPENDICES

APPENDIX A: Plants observed in study plots, including overstory and understory surveys. Organized by habit, family, genus, species (when not able to key to this level, genus only is listed), and susceptibility to *P. ramorum*. Nomenclature follows USDA Plants Database (plants.usda.gov).

Family	Scientific Name	Susceptibility to *P. ramorum*
Trees and Shrubs		
ACERACEAE	*Acer pennsylvanicum* L.	Possibly foliar (Garbelotto & Rizzo 2005), and seedling (Tooley & Kyde 2007)
	Acer rubrum L.	Possibly foliar (Garbelotto & Rizzo 2005), and seedling (Tooley & Kyde 2007)
	Acer saccharum Marsh.	Possibly foliar (Garbelotto & Rizzo 2005), and seedling (Tooley & Kyde 2007)
AQUIFOLIACEAE	*Ilex montana* Torr. & A. Gray ex A. Gray	Maybe, Canadian relative
BETULACEAE	*Betula alleghaniensis* Britton	
	Betula lenta L.	
CLETHRACEAE	*Clethra acuminata* Michx.	
CORNACEAE	*Cornus alterniflora* L. f.	Possibly, European relative
ERICACEAE	*Gaylussacia ursina* (M.A. Curtis) Torr. & A. Gray ex A. Gray	Foliar likely (Tooley, Kyde, and Englander 2004)
	Kalmia latifolia L.	USDA report says Europe, Foliar confirmed, highly susceptible (Tooley, Kyde, and Englander 2004) May provide innoculum (Tooley, Kyde, and Englander 2004).
	Oxydendrum arboreum (L.) DC.	Probably, need ref.
	Rhododendron calendulaceum (Michx.) Torr.	Foliar confirmed, poss. stem dieback and/or mortality (Werres et al. 2001, Tooley, Kyde, and Englander 2004) May provide innoculum (Tooley, Kyde, and Englander 2004).
	Rhododendron maximum L.	Foliar confirmed, possibly stem dieback or mortality (Werres et al. 2001, Tooley, Kyde, and Englander 2004, Garbelotto & Rizzo 2005) May provide innoculum (Tooley, Kyde, and Englander 2004).
	Vaccinium corymbosum L.	Foliar, possibly leaves and branch dieback or mortality (Tooley, Kyde, and Englander 2004, Garbelotto & Rizzo 2005)
FABACEAE	*Robinia psuedoacacia* L.	
FAGACEAE	*Castanea dentata* (Marsh.) Borkh.	Probably, need ref.
	Fagus grandifolia Ehrh.	Probably, need ref.
	Quercus alba L.	Seedling mortality (Tooley & Kyde 2007)
	Quercus prinus L.	Seedling mortality(Tooley & Kyde 2007)
	Quercus rubra L.	Tree mortality (Brasier et al. 2004, Garbelotto & Rizzo 2005), Seedling (Tooley & Kyde 2007)
HAMAMELIDACEAE	*Hamamelis virginiana* L.	Yes, need reference
JUGLANDACEAE	*Carya alba* (L.) Nutt. (formerly *C. tomentosa)*	
	Carya glabra (Mill.) Sweet	
LAURACEAE	*Sassafras albidum* (Nutt.) Nees	Possibly, same family as CA bay laurel
MAGNOLIACEAE	*Liriodendron tulipifera* L.	Maybe, Magnolias regulated
	Magnolia acuminata (L.) L.	Maybe, relative infected M grandiflora
	Magnolia fraseri Walter	Maybe, relative infected M grandiflora
	Magnolia virginiana L.	Maybe, relative infected M grandiflora
NYSSACEAE	*Nyssa sylvatica* Marsh.	

Family	Scientific Name	Susceptibility to P. ramorum
OLEACEAE	*Fraxinus pennsylvanica* Marsh.	Possible canker host, Europe (Rizzo et al 2005).
PINACEAE	*Tsuga canadensis* (L.) Carrière	
ROSACEAE	*Amelanchier arborea* (Michx. f.) Fernald	Would guess yes
	Amelanchier laevis Wiegand	Would guess yes
	Prunus serotina Ehrh.	Maybe, relative infected in same genus
	Rubus L.	Foliar (Garbelotto & Rizzo 2005)
SANTALACEAE	*Pyrularia pubera* Michx.	
Vines		
ARISTOLOCHIACEAE	*Aristolochia macrophylla* Lam.	
SMILACACEAE	*Smilax glauca* Walter	
	Smilax rotundafolia L.	
Herbaceous		
ASTERACEAE	*Aster* L.	
	Eupatorium fistulosus (Barratt) King & H. Rob.	
	Prenanthes L.	
	Solidago L.	
DIAPENSIACEAE	*Galax urceolata* (Poir.) Brummitt	
DIOSCOREACEAE	*Dioscorea villosa* L.	
EUPHORBIACEAE	*Euphorbia* L.	
GENTIANACEAE	*Gentiana* L.	
LILIACEAE	*Clintonia umbellulata* (Michx.) Morong	Foliar, possibly leaves and branch dieback (Garbelotto & Rizzo 2005)
	Medeola virginiana L.	Would guess yes
	Maianthemum F.H. Wigg.	Yes, need reference
	Prosartes lanuginosa (Michx.) D. Don	Would guess yes
	Streptopus lanceolatus (Aiton) Reveal	Would guess yes
	Trillium catesbaei Elliot	Would guess yes
	Uvularia perfoliata L.	Would guess yes
	Uvularia sessilifolia L.	Would guess yes
	Veratrum latifolium (Desr.) Zomlefer	Would guess yes
MONOTROPACEAE	*Monotropa hypopithys* L.	
	Monotropa uniflora L.	
ORCHIDACEAE	*Corallorhiza odontorhiza* (Willd.) Poir.	
	Goodyera pubescens (Willd.) R. Br.	
OROBANCHACEAE	*Conopholis Americana* (L.) Wallr.	
SCROPHULARIACEAE	*Melampyrum lineare* Desr.	
PYROLACEAE	*Pyrola americana* Sweet	
	Chimaphila maculata (L.) Pursh	
RUBIACEAE	*Houstonia purpurea* L.	
	Mitchella repens L.	
RUSCACEAE	*Polyganatum biflorum* (Walter) Elliot	
VIOLACEAE	*Viola hastata* Michx.	
	Viola L.	
UNKNOWN	Six unknown dicots	
Ferns		
OSMUNDACEAE	*Osmunda cinnomomea* L.	
	Osmunda claytoniana L.	
THELYPTERIDACEAE	*Thelypteris noveboracensis* (L.) Nieuwl.	
DRYOPTERIDACEAE	*Athyrium filix-femina* (L.) Roth ssp. *asplenioides* (Michx.) Hultén	Foliar, possibly leaves and branch dieback or mortality (Garbelotto & Rizzo 2005)
	Cystopteris bulbifera (L.) Bernh.	Foliar, possibly leaves and branch dieback or mortality (Garbelotto & Rizzo 2005)
Gramminoids		
CYPERACEAE	*Carex* L.	
	Two unknown gramminoids	
	Three unknown grasses	

APPENDIX B: Pre-treatment basal area and stand density. Organized by species and treatment, with standard deviation and percentage of total for both measurements.

		Basal area (m2/ha)			No. Stems /ha		
	Treatment	BA	SD	%	No.	SD	%
Acer pennsylvanicum	Control	0.01	0.01	0.02	29.6	32.1	0.5
	Girdle Only	0.27	0.45	0.76	44.4	67.6	0.8
	Girdle + Removal	0.12	0.16	0.34	44.4	19.2	1.0
Acer rubrum	Control	9.84	2.96	24.50	222.2	40.1	3.9
	Girdle Only	7.24	4.21	20.64	118.5	57.0	2.0
	Girdle + Removal	6.21	3.24	17.94	163.0	46.3	3.7
Acer saccharum	Control	0.00	0.00	0.01	3.7	6.4	0.1
	Girdle Only	0.03	0.05	0.08	18.5	32.1	0.3
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Amelanchier arborea	Control	0.07	0.02	0.17	33.3	19.2	0.6
	Girdle Only	0.05	0.07	0.13	11.1	11.1	0.2
	Girdle + Removal	0.09	0.12	0.25	14.8	17.0	0.3
Betula alleghaniensis	Control	0.00	0.00	0.01	3.7	6.4	0.1
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.13	0.11	0.38	29.6	42.1	0.7
Betula lenta	Control	2.10	0.10	5.23	59.3	12.8	1.0
	Girdle Only	1.91	1.95	5.45	33.3	40.1	0.6
	Girdle + Removal	0.82	0.99	2.37	29.6	32.1	0.7
Carya alba	Control	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.40	0.69	1.15	3.7	6.4	0.1
Carya glabra	Control	2.41	1.50	5.99	40.7	28.0	0.7
	Girdle Only	2.29	3.03	6.52	40.7	44.9	0.7
	Girdle + Removal	0.90	1.56	2.60	18.5	32.1	0.4
Castanea dentata	Control	0.17	0.15	0.43	177.8	123.7	3.1
	Girdle Only	0.02	0.04	0.07	40.7	44.9	0.7
	Girdle + Removal	0.00	0.00	0.00	18.5	23.1	0.4
Clethra acuminata	Control	0.05	0.08	0.12	270.4	468.3	4.7
	Girdle Only	0.03	0.05	0.09	85.2	147.5	1.4
	Girdle + Removal	0.03	0.04	0.07	196.3	340.0	4.5
Fagus grandifolia	Control	0.04	0.07	0.09	14.8	25.7	0.3
	Girdle Only	0.06	0.11	0.18	3.7	6.4	0.1
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Fraxinus pennsylvanica	Control	0.00	0.00	0.00	7.4	12.8	0.1
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Gaylussacia ursina	Control	0.00	0.00	0.00	11.1	19.2	0.2
	Girdle Only	0.01	0.01	0.02	81.5	131.6	1.4
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Hamamelis virginiana	Control	0.74	0.68	1.84	614.8	594.5	10.7
	Girdle Only	0.49	0.76	1.40	388.9	635.5	6.6
	Girdle + Removal	0.62	0.25	1.79	629.6	366.7	14.3
Ilex montana	Control	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle Only	0.19	0.32	0.53	70.4	121.9	1.2
	Girdle + Removal	0.23	0.38	0.66	151.9	224.8	3.5

		Basal area (m2/ha)			No. Stems /ha		
	Treatment	BA	SD	%	No.	SD	%
Kalmia latifolia	Control	0.63	1.09	1.57	374.1	628.8	6.5
	Girdle Only	0.14	0.23	0.38	59.3	102.6	1.0
	Girdle + Removal	0.08	0.11	0.24	77.8	90.9	1.8
Liriodendron tulipifera	Control	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.04	0.07	0.11	7.4	12.8	0.2
Magnolia acuminata	Control	0.03	0.05	0.07	14.8	17.0	0.3
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.00	0.00	0.01	3.7	6.4	0.1
Magnolia fraseri	Control	0.28	0.48	0.70	18.5	23.1	0.3
	Girdle Only	0.07	0.11	0.19	11.1	19.2	0.2
	Girdle + Removal	0.01	0.01	0.02	7.4	12.8	0.2
Magnolia virginiana	Control	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle Only	0.04	0.07	0.11	3.7	6.4	0.1
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Nyssa sylvatica	Control	0.71	1.20	1.77	33.3	29.4	0.6
	Girdle Only	0.05	0.08	0.13	7.4	12.8	0.1
	Girdle + Removal	1.97	3.32	5.68	22.2	29.4	0.5
Oxydendrum arboreum	Control	0.65	0.95	1.63	48.1	28.0	0.8
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Prunus serotina	Control	0.24	0.27	0.60	18.5	6.4	0.3
	Girdle Only	0.00	0.00	0.00	3.7	6.4	0.1
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Pyrularia pubera	Control	0.02	0.01	0.05	114.8	32.1	2.0
	Girdle Only	0.00	0.01	0.01	11.1	19.2	0.2
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0
Quercus alba	Control	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	2.22	3.85	6.43	22.2	38.5	0.5
Quercus prinus	Control	4.91	3.05	12.23	55.6	38.5	1.0
	Girdle Only	9.96	7.31	28.38	63.0	39.0	1.1
	Girdle + Removal	3.80	3.20	10.98	29.6	17.0	0.7
Quercus rubra	Control	10.14	2.87	25.26	125.9	54.8	2.2
	Girdle Only	9.57	2.96	27.26	63.0	44.9	1.1
	Girdle + Removal	13.26	6.65	38.32	70.4	39.0	1.6
Rhododendron calendulaceum	Control	0.25	0.20	0.62	525.9	487.2	9.2
	Girdle Only	0.11	0.06	0.30	363.0	170.8	6.1
	Girdle + Removal	0.17	0.26	0.48	485.2	640.4	11.0
Rhododendron maximum	Control	4.86	5.56	12.09	1855.6	930.2	32.3
	Girdle Only	2.46	0.45	7.00	1803.7	246.0	30.5
	Girdle + Removal	2.07	0.09	5.97	1451.9	265.1	33.1
Robinia psuedoacacia	Control	1.62	1.42	4.04	33.3	19.2	0.6
	Girdle Only	0.00	0.00	0.00	11.1	11.1	0.2
	Girdle + Removal	0.18	0.31	0.52	7.4	12.8	0.2
Rubus sp.	Control	0.00	0.00	0.00	22.2	38.5	0.4
	Girdle Only	0.00	0.00	0.00	929.6	1591.0	15.7
	Girdle + Removal	0.00	0.00	0.00	0.0	0.0	0.0

		Basal area (m2/ha)			No. Stems /ha		
	Treatment	BA	SD	%	No.	SD	%
Simlax rotundafolia	Control	0.06	0.10	0.16	881.5	1440.7	15.4
	Girdle Only	0.03	0.05	0.09	437.0	600.9	7.4
	Girdle + Removal	0.00	0.00	0.00	22.2	38.5	0.5
Tsuga canadensis	Control	0.08	0.13	0.19	14.8	25.7	0.3
	Girdle Only	0.09	0.16	0.27	3.7	6.4	0.1
	Girdle + Removal	0.30	0.37	0.88	25.9	28.0	0.6
Vaccinium corymbosum	Control	0.01	0.01	0.04	103.7	61.2	1.8
	Girdle Only	0.00	0.01	0.01	1200.0	2021.0	20.3
	Girdle + Removal	0.01	0.02	0.04	837.0	1257.5	19.1
Unknown	Control	0.23	0.22	0.57	7.4	6.4	0.1
	Girdle Only	0.00	0.00	0.00	0.0	0.0	0.0
	Girdle + Removal	0.96	1.66	2.77	22.2	38.5	0.5
Total	Control	40.16	7.48	100.00	5737.0	1856.6	100.0
	Girdle Only	35.09	12.98	100.00	5907.4	1024.8	100.0
	Girdle + Removal	34.59	10.44	100.00	4392.6	161.9	100.0

Appendix C: Mean number of seedlings per meter square. Includes standard deviation, and percentage of total by family, species, and treatment for each sampling period.

		Aceraceae			Aqulifoliaceae			Betulaceae			Clethraceae			Cornaceae		
		Acersp			Ilexmont			Betualle			Cletacum			Cornalte		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	1.9	1.2	35.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	3.9	1.8	77.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	1.9	2.6	39.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.9	0.0	0.0	0.0
Summer 2006	Control	0.5	0.2	10.7	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.1	0.1	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.3	0.1	5.7	0.0	0.0	0.5	0.0	0.0	0.5	0.1	0.1	1.9	0.0	0.0	0.0
Summer 2007	Control	0.9	0.6	18.5	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.9	0.7	23.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	1.4	1.4	17.0	0.1	0.1	0.8	0.0	0.0	0.0	0.4	0.3	4.4	0.0	0.0	0.0
Fall 2005	Control	0.5	0.1	2.8	0.0	0.0	0.1	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.2	0.1	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.1	0.1	3.8	0.1	0.1	2.5	0.0	0.0	0.0	0.0	0.1	1.3	0.0	0.0	0.0
Fall 2006	Control	0.5	0.5	1.4	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.1	0.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.1	0.1	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	2.3	0.0	0.0	0.0
Fall 2007	Control	0.8	0.5	2.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.8	0.7	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
	Girdle + Removal	1.1	0.8	18.2	0.0	0.1	0.7	0.0	0.0	0.3	0.3	0.4	4.3	0.0	0.0	0.0

		Ericaceae														
		Gaylursi			Kalmlati			Rhodcale			Rhodmaxi			Vaccsp		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	NA	NA	NA	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.4	8.8	0.0	0.0	0.4
	Girdle Only	NA	NA	NA	0.0	0.0	0.0	0.1	0.1	1.7	0.2	0.1	4.1	0.0	0.0	0.0
	Girdle + Removal	NA	NA	NA	0.0	0.0	0.0	0.4	0.3	7.2	0.7	0.8	14.5	0.0	0.0	0.0
Summer 2006	Control	NA	NA	NA	0.0	0.0	0.0	0.1	0.2	2.2	0.5	0.4	10.2	0.0	0.0	0.0
	Girdle Only	NA	NA	NA	0.0	0.0	0.0	0.1	0.1	3.9	0.1	0.1	5.5	0.0	0.0	0.0
	Girdle + Removal	NA	NA	NA	0.0	0.0	0.0	0.4	0.3	8.0	0.8	0.8	17.0	0.0	0.0	0.0
Summer 2007	Control	NA	NA	NA	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	7.3	0.0	0.0	0.4
	Girdle Only	NA	NA	NA	0.0	0.0	0.0	0.1	0.2	2.8	0.1	0.1	3.4	0.0	0.0	0.0
	Girdle + Removal	NA	NA	NA	0.0	0.0	0.0	0.4	0.4	5.2	2.1	3.1	26.1	0.0	0.0	0.3
Fall 2005	Control	14.2	7.1	78.8	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.9	0.0	0.0	0.0
	Girdle Only	7.8	1.8	76.4	0.0	0.0	0.0	0.1	0.1	1.0	0.1	0.0	1.0	0.0	0.0	0.0
	Girdle + Removal	0.0	0.0	0.6	0.1	0.1	1.9	0.0	0.1	1.3	0.3	0.1	7.6	0.0	0.0	0.0
Fall 2006	Control	31.8	20.9	87.7	0.0	0.0	0.0	0.2	0.3	0.5	0.3	0.3	0.9	0.0	0.0	0.0
	Girdle Only	15.1	6.3	90.1	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.1	0.7	0.0	0.0	0.0
	Girdle + Removal	0.1	0.1	2.3	0.0	0.1	0.9	0.4	0.5	8.3	1.0	1.4	22.9	0.0	0.0	0.0
Fall 2007	Control	32.7	18.0	85.9	0.0	0.0	0.0	0.1	0.3	0.4	0.5	0.4	1.2	0.0	0.1	0.1
	Girdle Only	15.9	7.8	84.6	0.0	0.0	0.0	0.1	0.1	0.3	0.2	0.1	1.0	0.0	0.0	0.0
	Girdle + Removal	0.1	0.1	1.0	0.0	0.0	0.0	0.3	0.3	5.3	1.4	1.9	21.5	0.0	0.0	0.0

		Fabaceae			Fagaceae											
		Robipsue			Castdent			Queralba			Querprin			Querrubr		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	0.0	0.0	0.0	0.1	0.1	1.5	0.0	0.0	0.0	0.0	0.0	0.4	1.3	1.4	23.1
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.5	5.8
	Girdle + Removal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	3.4	0.6	0.5	11.5
Summer 2006	Control	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.1	8.0	1.6	1.5	35.1
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	3.9	0.5	0.7	18.8
	Girdle + Removal	0.0	0.0	0.5	0.0	0.0	0.0	0.3	0.6	7.5	0.1	0.2	2.4	0.9	0.4	19.3
Summer 2007	Control	0.0	0.0	0.0	0.1	0.1	1.3	0.0	0.0	0.0	0.1	0.2	2.1	1.6	1.9	33.5
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.6	11.3
	Girdle + Removal	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	1.6	0.3	0.3	3.4	0.8	0.6	9.4
Fall 2005	Control	0.0	0.0	0.0	0.1	0.1	0.3	0.2	0.3	1.0	0.3	0.0	1.6	1.7	1.7	9.6
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.3	3.1	1.0	1.2	9.8
	Girdle + Removal	0.0	0.0	0.0	0.0	0.0	0.6	0.2	0.3	5.1	0.2	0.2	5.1	1.2	0.6	36.7
Fall 2006	Control	0.0	0.0	0.0	0.1	0.1	0.2	0.0	0.0	0.1	0.2	0.1	0.5	1.7	1.7	4.7
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.4	0.7	1.1	4.2
	Girdle + Removal	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.5	6.9	0.1	0.1	3.2	1.1	0.5	23.4
Fall 2007	Control	0.0	0.0	0.0	0.1	0.1	0.2	0.0	0.0	0.0	0.2	0.2	0.4	1.7	1.8	4.4
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.6	0.9	3.1
	Girdle + Removal	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.3	3.0	0.2	0.1	2.6	1.0	0.7	15.5

		Hamamelidaceae			Juglandaceae						Lauraceae		
		Hamavirg			Caryglab			Carytome			Sassalbi		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	0.4	0.3	6.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.1	0.1	2.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.7	0.8	14.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Summer 2006	Control	0.3	0.3	6.7	0.0	0.0	0.4	0.0	0.1	0.9	0.0	0.0	0.0
	Girdle Only	0.3	0.4	10.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.4	0.4	9.9	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
Summer 2007	Control	0.2	0.2	3.9	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
	Girdle Only	0.2	0.3	6.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.8	0.5	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
Fall 2005	Control	0.1	0.1	0.5	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.2	0.2	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.3	0.1	8.2	0.0	0.1	1.3	0.0	0.0	0.0	0.0	0.0	0.0
Fall 2006	Control	0.1	0.1	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.2	0.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.4	0.2	9.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
Fall 2007	Control	0.2	0.2	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.2	0.3	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle + Removal	0.7	0.6	10.9	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.3

		Magnoliaceae									Nyssaceae		
		Lirituli			Magnacum			Magnfras			Nysssylv		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.0	0.1	0.8	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4
	Girdle + Removal	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Summer 2006	Control	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.3	34.4
	Girdle + Removal	0.0	0.0	0.9	0.0	0.0	0.5	0.0	0.0	0.0	0.2	0.1	5.2
Summer 2007	Control	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	2.3	37.3
	Girdle + Removal	0.2	0.1	2.9	0.1	0.1	1.0	0.0	0.0	0.0	0.2	0.2	2.1
Fall 2005	Control	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.2	1.8
	Girdle + Removal	0.0	0.0	0.0	0.1	0.1	1.9	0.0	0.0	0.0	0.2	0.1	5.1
Fall 2006	Control	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2
	Girdle + Removal	0.0	0.0	0.9	0.1	0.1	1.8	0.0	0.0	0.0	0.1	0.1	2.8
Fall 2007	Control	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.7	2.8
	Girdle + Removal	0.1	0.1	1.7	0.1	0.1	1.0	0.0	0.0	0.0	0.1	0.2	2.3

		Roseaceae									Santalaceae			Aristolochiaceae		
	Treatment	Amelsp			Prunsero			Rubusp			Pyrupube			Isotduro		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	0.4	0.3	6.5	0.4	0.5	8.1	0.0	0.0	0.0	0.1	0.1	1.5	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.1	0.1	1.7
	Girdle + Removal	0.3	0.2	5.1	0.0	0.0	0.4	0.0	0.0	0.0	0.1	0.1	1.3	0.0	0.0	0.0
Summer 2006	Control	0.3	0.1	6.2	0.4	0.2	9.3	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.4
	Girdle Only	0.0	0.1	1.6	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	5.5
	Girdle + Removal	0.5	0.3	11.3	0.1	0.1	3.3	0.0	0.0	0.0	0.1	0.1	1.4	0.0	0.0	0.5
Summer 2007	Control	0.5	0.4	9.4	0.4	0.2	8.2	0.0	0.0	0.0	0.0	0.1	0.9	0.0	0.0	0.0
	Girdle Only	0.1	0.1	1.7	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	4.0
	Girdle + Removal	1.0	0.5	12.3	0.1	0.1	0.8	0.0	0.0	0.0	0.1	0.1	1.0	0.0	0.0	0.3
Fall 2005	Control	0.2	0.0	0.9	0.2	0.1	0.9	0.0	0.0	0.1	0.1	0.1	0.3	0.0	0.0	0.0
	Girdle Only	0.1	0.0	0.8	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.4
	Girdle + Removal	0.3	0.2	8.9	0.1	0.1	1.9	0.0	0.0	0.0	0.1	0.1	2.5	0.0	0.0	0.6
Fall 2006	Control	0.1	0.0	0.3	0.5	0.2	1.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.1	0.5
	Girdle + Removal	0.3	0.1	6.4	0.0	0.1	0.9	0.0	0.0	0.0	0.1	0.1	1.8	0.0	0.0	0.5
Fall 2007	Control	0.3	0.2	0.8	0.5	0.2	1.4	0.0	0.0	0.0	0.1	0.1	0.2	0.0	0.0	0.0
	Girdle Only	0.0	0.0	0.2	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.4
	Girdle + Removal	0.3	0.3	4.0	0.1	0.1	2.0	0.0	0.0	0.0	0.1	0.1	1.7	0.0	0.0	0.0

		Smilacaceae						All species		
		Smilglau			Smilrotu			Total		
Sampling Period	Treatment	No.	SD	%	No.	SD	%	No.	SD	%
Spring 2007	Control	0.0	0.0	0.0	0.4	0.6	7.7	5.4	0.8	100.0
	Girdle Only	0.0	0.0	0.0	0.2	0.2	4.1	5.0	2.5	100.0
	Girdle + Removal	0.0	0.0	0.0	0.1	0.1	1.7	4.9	2.4	100.0
Summer 2006	Control	0.0	0.0	0.4	0.4	0.6	8.4	4.7	0.6	100.0
	Girdle Only	0.0	0.1	1.6	0.3	0.3	10.2	2.7	0.6	100.0
	Girdle + Removal	0.0	0.0	0.0	0.1	0.2	3.3	4.4	2.4	100.0
Summer 2007	Control	0.1	0.1	2.1	0.5	0.7	10.3	4.9	0.3	100.0
	Girdle Only	0.0	0.0	0.0	0.4	0.5	9.6	3.7	2.0	100.0
	Girdle + Removal	0.0	0.0	0.0	0.1	0.2	1.8	8.0	3.2	100.0
Fall 2005	Control	0.0	0.0	0.1	0.3	0.2	1.4	18.0	8.2	100.0
	Girdle Only	0.0	0.0	0.0	0.2	0.1	1.6	10.2	2.8	100.0
	Girdle + Removal	0.0	0.0	0.0	0.1	0.1	3.2	3.3	1.4	100.0
Fall 2006	Control	0.2	0.3	0.5	0.5	0.7	1.5	36.3	21.6	100.0
	Girdle Only	0.0	0.0	0.0	0.3	0.3	1.5	16.8	7.4	100.0
	Girdle + Removal	0.0	0.0	0.0	0.1	0.1	2.3	4.5	2.5	100.0
Fall 2007	Control	0.1	0.1	0.2	0.8	0.8	2.0	38.0	18.8	100.0
	Girdle Only	0.0	0.0	0.1	0.3	0.4	1.8	18.8	7.8	100.0
	Girdle + Removal	0.0	0.0	0.3	0.2	0.2	3.0	6.3	3.0	100.0

APPENDIX D: Results of vegetation ANOVAs.

Richness - Summers Only, The GLM Procedure, Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**
treatment	2	785.240741	392.620370	6.62	0.0038
Error	33	1957.750000	59.325758		

Richness - Repeated Measures Summers Only, The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

						Adj Pr > F	
Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**	**G -G**	**H -F**
time	2	13.4074074	6.7037037	2.63	0.0797	0.0885	0.0822
time*treatment	4	13.5925926	3.3981481	1.33	0.2672	0.2715	0.2685
Error(time)	66	168.3333333	2.5505051				

Woody Richness - Repeated Measures Falls Only, The GLM Procedure, Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**
treatment	2	95.6296296	47.8148148	3.85	0.0314
Error	33	409.6666667	12.4141414		

Woody Richness - Repeated Measures Falls Only, The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

						Adj Pr > F	
Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**	**G -G**	**H -F**
time	2	8.07407407	4.03703704	2.68	0.0759	0.0792	0.0759
time*treatment	4	13.25925926	3.31481481	2.20	0.0782	0.0824	0.0782
Error(time)	66	99.33333333	1.50505051				

Greenhouse-Geisser Epsilon	0.9454
Huynh-Feldt Epsilon	1.0619

Herbaceous Species - Repeated Measures, The GLM Procedure, Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
treatment	2	80.5277778	40.2638889	2.79	0.0759
Error	33	476.0833333	14.4267677		

Herbaceous Species - Repeated Measures , The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
time	1	10.88888889	10.88888889	4.30	0.0460
time*treatment	2	9.52777778	4.76388889	1.88	0.1684
Error(time)	33	83.58333333	2.53282828		

Total Cover - Repeated Measures Springs Only, The GLM Procedure, Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
treat	2	12103.00000	6051.50000	5.13	0.0115
Error	33	38912.50000	1179.16667		

Total Cover - Repeated Measures Springs Only, The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
time	1	820.125000	820.125000	5.02	0.0319
time*treatment	2	128.583333	64.291667	0.39	0.6778
Error(time)	33	5391.791667	163.387626		

Total Cover - Repeated Measures Summers Only, The GLM Procedure
Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
treatment	2	18948.5729	9474.2865	2.81	0.0743
Error	33	111070.5990	3365.7757		

Total Cover - Repeated Measures Summers Only, The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

						Adj Pr > F	
Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**	**G -G**	**H -F**
time	3	4032.421875	1344.140625	15.81	<.0001	<.0001	<.0001
time*treatment	6	488.802083	81.467014	0.96	0.4576	0.4523	0.4576
Error(time)	99	8417.088542	85.021096				

Seedlings with Gaylussacia - Repeated Measures, The GLM Procedure, Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
treatment	2	197841.5556	98920.7778	6.76	0.0035
Error	33	482567.3611	14623.2534		

Seedlings with Gaylussacia - Repeated Measures, The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

						Adj Pr > F	
Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**	**G -G**	**H -F**
time	2	36641.16667	18320.58333	21.59	<.0001	<.0001	<.0001
time*treatment	4	19423.11111	4855.77778	5.72	0.0005	0.0042	0.0032
Error(time)	66	55993.72222	848.38973				

Greenhouse-Geisser Epsilon	0.6050
Huynh-Feldt Epsilon	0.6537

Seedlings without Gaylussacia - Repeated Measures Falls Only, The GLM Procedure Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
treatment	2	1995.018519	997.509259	3.78	0.0332
Error	33	8701.750000	263.689394		

Seedlings without Gaylussacia - Repeated Measures Falls Only, The GLM Procedure Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

						Adj Pr > F	
Source	**DF**	**Type III SS**	**Mean Square**	**F Value**	**Pr > F**	**G -G**	**H -F**
time	2	893.574074	446.787037	15.28	<.0001	<.0001	<.0001
time*treatment	4	355.259259	88.814815	3.04	0.0232	0.0351	0.0299
Error(time)	66	1929.833333	29.239899				

Greenhouse-Geisser Epsilon	0.7861
Huynh-Feldt Epsilon	0.8686

Seedlings without Gaylussacia - Repeated Measures Summers Only, The GLM Procedure, Repeated Measures Analysis of Variance, Tests of Hypotheses for Between Subjects Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
treat	2	1777.69444	888.84722	2.61	0.0887
Error	33	11239.41667	340.58838		

Seedlings without Gaylussacia - Repeated Measures Summers Only, The GLM Procedure, Repeated Measures Analysis of Variance, Univariate Tests of Hypotheses for Within Subject Effects

Source	DF	Type III SS	Mean Square	F Value	Pr > F
time	1	722.000000	722.000000	8.18	0.0073
time*treatment	2	599.083333	299.541667	3.39	0.0457
Error(time)	33	2912.916667	88.270202		

APPENDIX E: Results of litterfall ANOVAs.

LITTER:The ANOVA Procedure

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	20	386658.0079	19332.9004	Infty	<.0001
Error	159	0.0000	0.0000		
Corrected Total	179	386658.0079			

R-Square	Coeff Var	Root MSE	Mean weight
1.000000	0	0	43.52478

Source	DF	Anova SS	Mean Square	F Value	Pr > F
Treatment	2	19811.5411	9905.7706	Infty	<.0001
Category	4	241318.7218	60329.6804	Infty	<.0001
Category, Treatment	14	275502.1905	19678.7279	Infty	<.0001

Tukey's Studentized Range (HSD) Test for weight

Means with the same letter are not significantly different.			
Tukey Grouping	Mean	N	Treatment
A	54.85	60	Girdle-only
B	46.16	60	Control
C	29.56	60	Girdle + Removal scenario

Means with the same letter are not significantly different.			
Tukey Grouping	Mean	N	Category, Treatment
A	129.6	12	Other leaves, Control
B	111.5	12	Other leaves, Girdle-only
C	85.4	12	Other leaves, Girdle + Removal scenario
D	68.9	12	Other Plant, Girdle-only
E	56.6	12	Red oaks, Girdle-only
F	47.1	12	Other Plant, Control
G	36.4	12	Red oaks, Control
H	36.1	12	Red oaks, Girdle + Removal scenario
I	34.2	12	Rhododendron, Girdle-only
J	24.1	12	Other Plant, Girdle + Removal scenario

K	16.1	12	Rhododendron, Control
L	2.9	12	Misc., Girdle-only
M	1.9	12	Misc., Girdle + Removal scenario
N	1.6	12	Misc., Control
O	0.3	12	Rhododendron, Girdle + Removal scenario

APPENDIX F: Results of soil ANOVAs.

Modeling Moisture versus time, cover and treatment
The Mixed Procedure

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Treatment	2	3497	58.79	<.0001
Cover	2	3497	219.7	<.0001
Time	22	3497	56.69	<.0001
Treatment*Cover	4	3497	67.08	<.0001
Treatment*Time	44	3497	1.21	0.1653
Cover*Time	44	3497	0.88	0.6935
Treatment*Cover*Time	88	3497	0.74	0.9659

Modeling Temperature versus time, cover and treatment
The Mixed Procedure

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Treatment	2	3468	132.57	<.0001
Cover	2	3468	67.62	<.0001
Time	22	3468	3925.53	<.0001
Treatment*Cover	4	3468	30.18	<.0001
Treatment*Time	44	3468	5.92	<.0001
Cover*Time	44	3468	3.91	<.0001
Treatment*Cover*Time	88	3468	1.29	0.0359

Modeling Efflux versus time, cover, treatment, moisture and temperature
The Mixed Procedure

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Treatment	2	3460	243.40	<.0001
Cover	2	3460	18.83	<.0001
Time	22	3460	122.73	<.0001
Treatment*Cover	4	3460	11.41	<.0001
Treatment*Time	44	3460	7.78	<.0001
Cover*Time	44	3460	1.95	0.0002
Treatment*Cover*Time	88	3460	1.46	0.0036
Soil Temperature	1	3460	34.52	<.0001
Soil Moisture	1	3460	46.97	<.0001

Modeling St_Efflux versus time, cover, treatment, moisture and temperature
The Mixed Procedure

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Treatment	2	3460	232.1	<.0001
Cover	2	3460	16.12	<.0001
Time	22	3460	115.65	<.0001
Treatment*Cover	4	3460	11.46	<.0001
Treatment*Time	44	3460	7.49	<.0001
Cover*Time	44	3460	1.78	0.0012
Treatment*Cover*Time	88	3460	1.39	0.0097
Soil Temperature	1	3460	0.13	0.72
Soil Moisture	1	3460	36.92	<.0001