Ecology, Competitive Advantages, and Integrated Control of Rhododendron: An Old Ornamental yet Emerging Invasive Weed Around the Globe

Derya E en1*, Erik T. Nilsen2, Oktay Yildiz1

1 Abant Izzet Baysal Üniversitesi, Düzce Orman Fakültesi (Forestry Faculty), Konuralp 81620, Düzce, Turkey
2 Virginia Tech, Department of Biological Sciences, Blacksburg, Virginia, 24061, USA

Corresponding author: * guzelfethiye@yahoo.com

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ABSTRACT

A dilemma surrounding Rhododendron confers upon this genus unique characters among plants. Great ornamental values (spectacular flowers, species-richness, ease of hybridization and broad geographical range) will continue to make Rhododendrons highly celebrated horticultural plants around the world. Their highly invasive ecophysiology (e.g. shade- and cold-tolerance, great resource use efficiency, allelopathy), life strategy (e.g. plastic physiological, morphological, and behavioral response to varying environments and shifting between generative and vegetative reproduction as primary source of colonization), and difficulty to control also will continue to make this shrub a notorious woody weed world-wide. This chapter focuses on the two most highly problematic Rhododendron species (R. ponticum L. and R. maximum L.) that exert profound impacts on natural ecosystems on both sides of the Atlantic. The broad geographical range and noteworthy similarities in climate, topography, and ecology of Rhododendron species can provide an opportunity to understand the ecology and control of invasive Rhododendron species. Information transfer on the ecology and effective, cost-efficient control of Rhododendron may significantly improve management practices not only for the current Rhododendron-invaded ecosystems but also for other parts of the world where this shrub is becoming an ecological threat.

1. INTRODUCTION

Rhododendron is a highly celebrated ornamental genus because of its spectacular flowers, species-richness, ease of hybridization and broad geographical range (Cox 2003, Evans 2003). Approximately 1000 species inhabit a vast geographical range, from the tropics to the polar zone and alpine to sea level (Chamberlain et al. 1996). However, some species of Rhododendron have recently come under scrutiny worldwide for adversely affecting natural forest dynamics and creating serious forest management problems. Many studies have reported significantly reduced canopy tree regeneration, tree growth and local biodiversity. Extensive site preparation expenses are incurred to minimize negative impacts of Rhododendron species on some forested sites. Moreover, habitat destruction in both urban and natural settings by Rhododendron ponticum L. (purple-flowered Rhododendron, or forest rose) has been documented throughout the Black Sea Region (termed BSR throughout this chapter) of Turkey (Fig. 1A; Çolak et al. 1998, E en and Zedaker 2004, E en et al. 2004 2006) and the United Kingdom (UK) (Fig. 1B; Cross 1975, Gritten 1995, Rotterdam 2003, Erfmeier and Bruelheide 2004), by Rhododendron maximum L. (great Rhododendron termed GR throughout this chapter) in the Southern Appalachians of the USA (Clinton et al. 1994, Lei et al. 2002, Nilsen and Horton 2003, Beier et al. 2005), and by Rhododendron albilorum Hook. (white-flowered Rhododendron) in Canada (Coats et al. 1991). The invasive potential of R. ponticum (termed PFR throughout this chapter) in Belgium, the Netherlands, and Northwest Germany is also recognized (Niinemets et al. 2003, Erfmeier and Bruelheide 2004). R. ponticum is not yet recognized as a major woody threat in Georgia, and it is not invasive and is even considered endangered in Spain (Blanca et al. 2000, Mejias et al. 2002, Erfmeier and Bruelheide 2004).

This chapter focuses on the two most highly problematic Rhododendron species (PFR and GR), exerting profound impacts on natural ecosystems on both sides of the Atlantic. The habitats of these two species in the BSR of Turkey, the Southern Appalachians of the US, and the UK, are similar in climate, topography, and general forest flora. Also, PFR and GR have similar ecology and are associated with similar forest vegetation problems (E en 2000, Nilsen and Horton 2003, E en et al. 2004). These functional similarities among species from different continental locations may be explained by the effects of the environment on development of certain traits used by plants to cope with their environments (Grime 1979). Stressful environments shape the composition of a plant community by applying a selective pressure on species (Perry 1997, Peterson and Jones 1997). Evergreen leaves, long-lived foliage, and vegetative reproduction are accepted as common adaptive
traits among plants that grow in stressful environments (Perry 1994, Jonasson 1995, Peterson and Jones 1997). Both, PFR and GR have many appropriate traits for stressful environments, probably owing to similar selective pressures of their respective environments (Een 2000, Nilsen and Horton 2003).

Rhododendrons’ adverse effects on forest productivity gain more significance in the light of presently increasing global demand for wood products and decreasing amount of land under wood production (Guynn et al. 2004). A recent study stated that PFR may expand on relatively drier site in the BSR, contrary to its common mesic character (Een et al. 2004). Current Rhododendron-dominated and threatened BSR ecosystems, where PFR is native, may provide an advanced ecological picture for the forests in the US and other countries in which Rhododendron species have become problematic. Global climate change and increasing N-deposition may further accelerate the current pace of Rhododendron invasion in the near future (Niinemets et al. 2003). This chapter aims to understand the underlying ecology, the invasive mechanism of Rhododendron species and to evaluate various woody control approaches for practical, effective, long-term, and cost-efficient control of this invasive woody species.

2. INVASION HISTORY

The primary native range of PFR (ssp. ponticum) is the BSR of northern Turkey, with disjunct occurrences in the Taurus Mountains in southern Turkey, the Western Caucasian Countries, and parts of Lebanon, Portugal, and Spain (Cross 1975, Rotherham 2003, Erfmeier and Bruehlheide 2004). In Turkey, this large, tall shrub (3 m in height) predominates the cool, mesic, northern slopes of the BSR to the Georgian border where annual precipitation averages 700-2,000 mm (Atalay 1992, Çolak 1997).

There have not been many historical records on PFR presence or its development in the BSR except one from the ancient Greek writer-traveler Xenophon from 405 B.C. Xenophon compiled his experiences and impressions about an area encompassing the BSR in his book called “Anabasis” while accompanying the Greek army on its campaign against the Persian army. A type of honey termed forestrose honey is commonly known and consumed in rural BSR. The honey is produced by bees that forage on Rhododendron pollen, and thus it is a specialty of the region. A bitter taste is characteristic of this honey, and when it is consumed in large quantities, it causes temporary abdominal illness. This honey brought the Greeks a quick and easy victory against the Persian army (Brownson 1980, Aksoy 1998, pers. com.). Although the natural range and local distribution cannot be derived from these accounts, it is likely that PFR has been present in the BSR for more than one millennium (Een 2000). Natural and artificial forest regeneration is virtually impossible in PFR dominated regions of the BSR without the control of this pernicious woody weed (Een and Zedaker 2004). This ‘neglected native’ (Rotherham 2003) has become a major threat to the BSR forest ecosystem (Een and Zedaker 2004).

PFR’s current distribution in Europe is mostly linked to ‘the Pleistocene Glaciations’ (Rotherham 2003). PFR in southern Spain is related to an evergreen rain forest that covered Europe during the Tertiary Period (Mejias et al. 2002). Although pollen studies indicate that PFR occurred in the British Isles during interglacial periods and disappeared following the last ice period (Cross 1975, Evans 2003), PFR was brought back to the UK in 1765 as an ornamental plant in large Victorian estates. PFR was used as an ornamental because of its growth form and spectacular
purple flowers. In addition, PFR was planted for game cover and shelterbelts (Cross 1975, Robinson 1980, Shaw 1984, Tabbush and Williamson 1987, Evans 2003, Rotherham 2003). The origin of the particular shrubs planted in Victorian estates was first thought to be the BSR: however, recent studies indicated that the British and Irish populations of PFR originated from the Iberian Peninsula (ssp. baeticum, Walker and Straka 1970, Tabbush and Williamson 1987, Abbott and Milne 1995, Milne and Abbott 2000, Rotherham 2003, Erfmeier and Bruelheide 2004). Following its planting in the Victorian estates PFR has since invaded much of the British and Irish landscape and has become a ‘naturalized invasive alien’ (Fig. 1B; Rotherham 2003). The shrub is considered one of the 20 most invasive weeds in the UK (Crawley 1987). Hybridization has been associated with the expansion of PFR populations in the UK.

Hybridization is a common phenomenon among Rhododendron species in natural environments (Chamberlain 2003). At least three different Rhododendron species have hybridized in the UK with the original PFR from the Iberian peninsula, including a North American relative, R. catawbiense Michaux. Hybridization has increased the genetic variation and competitive advantage of PFR in Europe (Milne and Abbott 2000, Chamberlain 2003, Niinemets et al. 2003, Rotherham 2003).

On the other side of the Atlantic, evergreen GR grows from the southeastern US (central Georgia) to the south of Canada along the Appalachian and Allegheny mountains, covering nearly 1.2 million hectares (Dobbs 1998, Clinton 2003, Nilsen and Horton 2003). It may reach 3-7 m in height and grows in dense populations (5-17,000 stems ha⁻¹). Similar to its Eurasian relative, GR prefers cool, moist northern slopes of mountains and stream banks (Baker 1994, Clinton et al. 1994, Baker and Van Lear 1998, Nilsen and Horton 2003). Historical accounts of the abundance and distribution of GR in the Southern Appalachians are rare (Baker 1994). Previous studies reported that this shrub was relatively limited in the past (mostly in riparian and other mesic zones) when compared to its present range (Baker 1994, Clinton 2003). Currently, GR grows from valley bottoms up north slopes and onto southerly exposures to some extent. Dobbs (1995) reported that this shrub increased its abundance in the region from 15% to 33% of the Crowetza Hydrologic Forest during 1976-1996. The general extent of GR cover has been increasing over the past one hundred years due to changes in forest composition and structure (McGivney 1972, Monk et al. 1985, Phillips and Murdy 1985).

Disturbances (both natural and anthropomorphic) are intimately involved with the expansion of Rhododendron species in recent history. The current species-rich Southern Appalachian forest has historically experienced many major disturbances (Nilsen and Horton 2003). The Native Americans made a major impact on the region’s forest, partially by cuttings and frequent burning. The pioneer settlers then continued disturbing the forest resources for food, fuel, shelter, and cultivation (Baker 1994). Recession of American chestnut (Castanea dentata) due to an epidemic of chestnut blight (Endothia parasitica) contributed significantly to creation of gaps in the overstory and in turn to an increase in GR invasion into these gaps (Baker 1994, Nilsen and Horton 2003). Furthermore, tree blow-downs have been recognized as an important disturbance agent of the Pocono ecosystem in Pennsylvania in which GR was a significant component (Latham et al. 1996). Also, the fire-exclusion policy of the region contributed to vigorous invasion of GR (Baker 1994) into drier habitats such as the upper reaches of north slopes and some southerly aspect sites (Dobbs 1998, Clinton 2003).

Disturbances, plant genotype, historical circumstances, climate, soil conditions, a lack of natural enemies and a decrease of labor-force in charge of controlling PFR have helped the recent, rapid invasion of PFR in the UK (Robinson 1980, Tabbush and Williamson 1987, Evans 2003, Erfmeier and Bruelheide 2004). However, it is clear that anthropogenic factors played a direct role in the spread of PFR. Promotion of this exotic species for aesthetic reasons in the UK and Ireland, at the beginning of the 18th century, contributed to the increase in PFR (Cross 1981, Gritten 1995). Moreover, the woody weed’s spread has been stimulated by long-lasting human disturbances in southwest Ireland (Cross 1981). Grazing, regardless of whether it is human-induced, is another major disturbance that might promote or depress the proliferation of PFR (Cross 1981). Low-intensity deer and sheep grazing in North Wales, UK, promoted PFR establishment by reducing competition from other plants (Cross 1981, Shaw 1984, Rotherham 1990, Thomson et al. 1993). Furthermore, low-intensity grazing can provide “safe sites” for PFR germination (Cross 1981, Tabbush and Williamson 1987). Displacement of vegetation and perturbation of soil by grazers, including deer, goat, sheep, cattle, and even birds, can create suitable conditions in the soil for bryophyte establishment. Bryophytes provide improved moisture and light conditions and protection from outside influences for PFR seed (Fig. 1C, Cross 1981, Tabbush and Williamson 1987). In contrast, high-intensity grazing with short return intervals suppressed the population spread of PFR (Rotherham 1990, Thomson et al. 1993, Baker 1994, Gritten 1995). Similar high-intensity grazing pressures were applied on PFR by native red deer (Cervus elaphus L.), domestic cattle, pigs, goats, sheep, and exotic sika deer (C. nippon) in the Killarney Oakwoods of southwest Ireland, hence preventing establishment of dense PFR populations (Cross 1981). Heavy grazing has had a negative impact on populations of other Rhododendron species. For example, Pomon and Doche (1995) observed that R. ferrugineum populations flourished only in the meadows of the northwestern Alps in France, where heavy grazing was not a significant disturbance. Grazing in conjunction with fire kept populations of GR low in the Southern Appalachians until the cessation of these disturbance agents around the 1920’s (Baker 1994, Phillips and Murdy 1985, Clinton and Vose 1996).

Fire is another disturbance whose effects on Rhododendron species spread is dependent upon its intensity and return interval. Colak (1997) performed a low-intensity burning trial on a PFR site in the BSR, Turkey. One year after application, results indicated that burning had suppressed PFR resprouting significantly. Following the second growing season after application, however, PFR sprouted prolifically from buds on the “ignotuber” roots (Colak 1997). Frequent and widespread fires in the eastern US between 1897 and 1917, along with other human-induced disturbances, prevented GR populations from spreading (Phillips and Murdy 1985, Baker 1994). Rhododendron populations were probably confined by fire within their natural boundaries, including riparian zones, mesic islands, riverbanks and other moisture-rich areas (Baker 1994). Also, another North American species (R. canadense (L.) Torr.) was found growing only in an ecotone between a fire-maintained scrub oak community and a fire-protected swamp forest in the Pocono plateau of Pennsylvania (Latham et al. 1966). Therefore, the fire suppression program put in effect in the eastern USA after the 1920’s, removed a check on aggressive GR populations, resulting in rapid expansion of this woody species (Monk et al. 1985, Philips and Murdy 1985, Baker 1994, Nowacki and Abrams 1994).

Fire was important in shaping today’s forests in the BSR (En et al. 2004). The Ottoman Empire, which had reigned in the region for nearly six centuries, traded widely and had extensive warship fleets. The Empire heavily relied on wood from the BSR forests where fire-dependent conifers made up a significant component. The abundance of fire dominated conifers suggests that fire was a major component of the historic BSR ecosystem. The continuous selective logging of conifers (which probably checked the excessive understory growth then with year-round
shade) and the long-term fire suppression policy of the Turkish Forest Service have shaped the composition and dynamics of the region’s forests and probably contributed to the expansion of PFR (Een 2000). Anthropogenic activities (e.g. clearings for cultivation, fuelwood, and animal husbandry) are currently the most important disturbances in the BSR used by PFR for range expansion (Çolak 1997, Een and Zedaker 2004).

![Graph 1](image1.png)

**Fig. 2** Frequency distributions of Rhododendron ponticum diameter (above) and age (below) in two different locations (Yayla and Devrek) in the western Black Sea Region of Turkey. Note the different scale of the X-axis. Reprinted from Een et al. (2004) Forest Ecology and Management 203, 229-240, © 2004, with permission from Elsevier.

3. STAND STRUCTURE AND PRODUCTIVITY

The problematic Rhododendron species we consider here share many similarities in stand characteristics. In its native range, PFR forms a dense (48,000–107,000 stems ha\(^{-1}\)) and a mean basal area of 14 m\(^2\) ha\(^{-1}\) and tall (2-5 m) green carpet in the understory of the mesic eastern beech (Fagus orientalis Lipsky) forests (Fig. 2; Een and Zedaker 2004, Een et al. 2004, Een, personal data). Rhododendron populations in the UK bear notable differences in stand structure, when compared to those in Turkey. Most invasive populations of PFR in the UK tend to have a high and variable density (1,000–10,000 stems ha\(^{-1}\)) with small diameters (<10 cm). Infrequently, there are populations of bushes that are at low density (<100 stems ha\(^{-1}\)) and large diameter (>30 cm) but these tend to be infrequent. Population densities tend to be great on the west coast but low on the east coast (Edwards 2005, pers. comm.). Populations of PFR in Ireland can be equally dense. In Spain and Georgia, where PFS is not problematic, stands can reach densities of 30,000 stems ha\(^{-1}\) and 55,000 stems ha\(^{-1}\) respectively (Erfmeier and Bruelheide 2004). Although not as widespread and problematic as PFR, deciduous yellow-flowered Rhododendron (R. luteum Sweet) established on high elevations of north- and south-faced aspects of the eastern BSR mountains, may have greater densities (90,000 stems ha\(^{-1}\)) than PFR (Çolak 1997, Een and Zedaker 2004). Also, GR in the southeastern US attains high population density (10,000 stems ha\(^{-1}\) with a mean groundline basal area of 14 m\(^2\) ha\(^{-1}\); Baker 1994).

Ground line diameter (GLD) distributions for stands of both PFR and GR characteristically have an inverse-J shape, indicating a regular uneven-aged stand structure for a shade-tolerant woody species (Baker 1994, Een et al. 2004). Tree diameter (or GLD) is commonly used instead of age for assessing stand vegetation structure. This may result in erroneous conclusions about the population growth because the relationship between diameter and age can be weak. In fact, diameter-age relationships are generally weak for shade-tolerant tree species (Smith et al. 1997). However, Rhododendron species have a strong correlation between GLD and age, indicating that the population structure of GLD could be a good estimator of population dynamics (Een et al. 2004). The reverse J-shaped population structure may result from vigorous regeneration following disturbance (Cross 1981, Shaw 1984, Een et al. 2004, Een and Zedaker 2004) causing the population size to increase ‘exponentially’ after disturbances (Möské et al. 1985, Baker 1994, Dobbs 1995, Hedman and Van Lear 1995). Moreover, the large fraction of Rhododendron individuals in smaller GLD classes suggests that this invasive shrub will continue to be problematic in both the BSR and the Southern Appalachians of the south eastern US (Baker 1994, Een et al. 2004).

PFR produced 0.7 kg m\(^{-2}\) total dry biomass in the understories of a Scots pine (Pinus sylvestris L.) stand in Belgium (Nadezhdina et al. 2004) and between 2.5 and 5.5 kg m\(^{-2}\) total dry biomass in the understories eastern beech stand in the BSR of Turkey (Yıldız and Een, 2005, Sargınç 2005). PFR allocated 40% of its total mass to below-ground parts (Sargınç 2005). Although Rhododendron leaf dry mass on both sites was similar (0.23–0.24 kg m\(^{-2}\)), the BSR population invested less carbon in foliage (4% of total mass) than the Belgian population (30% of total mass) (Nadezhdina et al. 2004, Sargınç 2005).
4. ECOPHYSIOLOGY

4.1. Shade tolerance

Available light under hardwood overstories is naturally below 10-15% of the available light in the open (Clinton and Vose 1996, Çolak 1997, En et al. 2004). This does not limit Rhododendron species from growing where many of their competitors succumb to insufficient light (Clinton and Vose 1996, Nilsen et al. 2001, Nilsen and Horton 2003). Rhododendron species in the understorey further reduce available light on the forest floor by 70-95% (Clinton et al. 1994, Çolak 1997, Nilsen et al. 2001, Clinton 2003, En et al. 2004). In fact, only 0.2-0.6% of the available light was found under GR and PFR canopies in mixed-hardwood forests of the eastern US and two eastern beechnuts sites in the BSR (Nilsen et al. 2001, En et al. 2004, respectively). Understorey light levels below a Rhododendron canopy are equivalent to that found in the understorey of mature tropical forests (Lei et al. 2005). These light levels are well below the photosynthetic light compensation point for many hardwood tree species (Larcher 1995, Semones 1999, Nilsen et al. 2001). Only a handful of plants can survive below the canopy of a GR or PFR stand, including Arbutus unedo, Ilex aquifolium, Taxus baccata, and Hedera helix (Cross 1981, Çolak 1997, En 2000).

Rhododendron species have relatively low light compensation points (Cross 1973). For example the light compensation point for GR in the southern Appalachian Mountains was 15-25% of incident light at 1000 W m⁻² (Bao and Nilsen 1988). Light compensation point for PFR, R. catawbiense, and R. minus in a common garden in south eastern US were 35, 25, and 22% of incident light respectively under moderately high light conditions and 15, 12, and 22% of incident light respectively under low light conditions (Lipscomb 1991). Therefore, Rhododendron species are able to maintain carbon gain to approximately 1% of full radiation (2000 W m⁻²). Moreover, light compensation points decrease with a decrease in light intensity (Lipscomb 1991). The high shade tolerance of Rhododendron species is linked to its low light compensation point (0.5-0.6 and less than 2% light, Çolak 1997 and Tabbush and Williamson 1987, respectively). And its ability to harvest diffuse light (Nilsen and Horton 2003).

Also, evergreen foliage allows the Rhododendron canopy to perform gas exchange during the early spring high solar radiation in hardwood stands (Tabbush and Williamson 1987).

Leaf abundance and display is important for the shade tolerance of Rhododendron species. A relatively high leaf area index (1.25) and leaf biomass (about 2.4 t ha⁻¹) are critical for Rhododendron species success in forest stands (Nadezhdina et al. 2004). Leaves are produced in even aged whorls usually only once per growing season. The leaves of the current year whorl are arranged to minimize self shading of the previous year whorl. In fact, in those species that have longer lived leaves (GR leaves can last up to 7 years) the older leaf cohorts are more pendant than the younger leaves to further minimize self shading among leaves. Therefore, understorey Rhododendron species have a maximum leaf area with minimum self shading.

Many Rhododendron species have extensive physiological, morphological, and behavioral plasticity (Niinemets et al. 2003). For example, PFR was found to have a greater resource use efficiency, investment of nitrogen in photosynthesis and phenotypic plasticity in foliage when compared to one of its shade tolerant companion woody species (Lipscomb and Nilsen 1990a). Leaf size, orientation, and leaf numbers per whorl can change drastically among sites with different light regimes. For example, leaf area increases from an average of 23.3 cm² to 52.5 cm² from a high light site to a shaded site for GR (Nilsen 1985). Moreover, the ratio of shoot wood to leaf area decreases from 440 g m⁻² to 150 g m⁻² in GR from high light to shady location (Lipscomb 1991). Therefore, Rhododendron species are able to maintain carbon gain to approximately 1% of full radiation (2000 W m⁻²). Moreover, light compensation points decrease with a decrease in light intensity (Lipscomb 1991). The high shade tolerance of Rhododendron species is linked to its low light compensation point (0.5-0.6 and less than 2% light, Çolak 1997 and Tabbush and Williamson 1987, respectively). And its ability to harvest diffuse light (Nilsen and Horton 2003).

Additionally, high direct solar radiation accelerated disintegration of leaf chlorophyll (Nilsen and Bao 1987) and induced the formation of plasto-globules (remnants of damaged membranes) in chloroplasts (Nilsen et al. 1988). Therefore, the optimum habitat for GR (and many other temperate species of Rhododendron) is the subcanopy of a moderately dense forest.

High shade tolerance should not devalue the importance of light for Rhododendron species. It is common for Rhododendron species to grow long and slender stems under circumstances where light is scarce (Nilsen 1986, Çolak 1997). An abundance of light (i.e., between 10 and 30% of full sun) is also essential for inflorescence formation for Rhododendron (Nilsen 1986, Çolak 1997). Therefore, seed production and dissemination take place predominantly in illuminated thickets, which grow in ecotones between the heavily shaded understory and the open (Çolak 1997, En 2000). Moreover, a preference for the subcanopy does not preclude these species from growing in full sun situations. A change in exposure from shady to sunny will severely damage Rhododendron plants causing leaf bleaching and stem death. However, if plants are cut back at the time of exposure change, the regrowth on Rhododendron plants is accelerated to high light and the plant can thrive. In fact, there are many dense covers of 100% Rhododendron plants at high elevation in the Southern Appalachian Mountains (heath balds) and in post clear cut sites at lower elevation. Also, PFR is able to produce dense stands without a canopy cover in the U.K.

4.2. Cold tolerance

Climatic conditions in their native habitat vary among Rhododendron species. In fact, the climatic conditions for the native habitats of PFR and GR are quite different. The native range for GR is continental resulting in moderately cold winters with frequent freezes and thaws. In contrast, the natural habitat of PFR is more maritime (particularly for the British Isles) resulting in fewer freeze thaw cycles and a more moderate temperature. In accordance with the difference in native climate, cold stress tolerance is better developed for GR (and R. catawbiense from the same region) than for PFR (and R. ungernii from the same region). The American Rhododendron Society ranks the hardness for GR and R. catawbiense at ~25°C while the hardness of PFR is rated at ~5°C. And R. ungernii is rated at ~10°C (Nilsen 1991, Nilsen and Tolbert 1993).
There are several reasons why GR has higher cold stress tolerance than PFR. The leaf freezing points for GR and R. catawbiense change from -1.5°C to -4.6°C from the summer to winter (Cordero and Nilsen 2002). Although this is a significant change in leaf freezing tolerance it does not explain the high cold tolerance (−25°C) of GR. Thermomastic leaf movements are highly correlated with hardness among species of Rhododendron (Nilsen and Tolbert 1993). Species with strong leaf curling in response to freezing (GR and R. catawbiense) are much more cold tolerant than those species with minimal leaf curling in response to freezing such as PFR (Nilsen 1991). There are many possible theories about the functional significance of thermomastic leaf movements, but the most accepted is that leaf curling and leaf drooping during freezing conditions protects the photosynthetic apparatus from damage during periods of low temperature and high light (Nilsen 1985, 1992).

Freeze-thawing cycles, characteristic of the southern Appalachian Mountains, put considerable stress on the vascular system of Rhododendron species. When water in the xylem freezes, gasses come out of solution. Upon thawing, these small gas bubbles can coalesce forming an embolism that blocks xylem elements, halting any flow of water. Freeze-thaw induced embolism is a well-known problem for vascular plants in regions with frequent freezes (Davis et al. 1999). Both GR and R. catawbiense can suffer 50% or more blockage of water flow in the xylem because of freeze-thaw events (Lipp and Nilsen 1997, Cordero and Nilsen 2002). However, following re-warming, both species are able to rapidly improve xylem flow by dissolving embolism in the vessel elements (Cordero and Nilsen 2002). We are unaware of any information on the vulnerability of PFR stems to freeze-thaw induced embolism.

One major structural adaptation to frequent freeze-thaw events is narrow vessels. Bubbles that form in a vessel after freezing will remain small and easier to force back into solution if the vessels are narrow (Davis et al. 1999). Vessel elements of GR, R. macrophyllum, and GR average close to 15 μm in diameter (Cordero and Nilsen 2002). These measurements are very small compared to other angiosperms. Therefore, many Rhododendron species of the temperate zone have narrow vessels to minimize the danger of freeze-thaw induced embolism and to repair the embolism if it occurs. These narrow vessels could become a liability during a summer drought.

Cold stress tolerance in PFR in the UK is enhanced from hybridization with R. catawbiense and GR. There is clear molecular evidence that the invasive PFR in the UK has greatest affinity with the PFR genotypes from the Iberian Peninsula (Milne and Abbot 2000). However, there is ample evidence that molecular signatures from GR and R. catawbiense are present in the PFR genotypes in the UK. Moreover, the proportion of PFR accessions with R. catawbiense or GR molecular markers increases as samples are taken further north (Milne and Abbot 2000). This suggests that the hybridization of PFR with the North American Rhododendron species has increased the cold tolerance of PFR in the UK.

4.3. Water relations

There are several traits of Rhododendron species that in combination make these species relatively sensitive to water limitations. First, leaves are relatively large and plants require a large whole plant leaf area to survive in the subcanopy environment. Second, the xylem vessels are relatively narrow and the vascular system is diffuse-porous with many non-conducting vessels. Third, the root system is shallow relative to many other shrubs of comparable size. Therefore, if stomata open significantly, there will be a large demand for water (large leaf area), but a limited ability to transport water (narrow vessels) and a limited ability to accumulate water from the soil (shallow roots). Due to this combination of traits, leaf conductance is low and flow in the xylem is limited (Lipp and Nilsen 1997). For example, stomata of GR close if the plant water potential approaches -1.5 MPa (Lipscomb and Nilsen 1990b). Moreover, stomatal conductance is usually below 100 mmol m⁻² s⁻¹, which is characteristic of plants in stressful environments (Nilsen and Orcutt 1996).

Osmotic adjustment could be a mechanism to maintain turgor (and keep stomata open) when leaf water potential is decreasing (due to high water demand of leaves and low water supply to leaves). We have found no significant osmotic adjustment in response to drought for GR in the southern Appalachian Mountains (Nilsen, pers. data). A small amount of osmotic adjustment (0.65 MPa) was found for GR in the Cumberland plateau of eastern Kentucky (Muller 1991). Theoretically, there is no reason to believe that osmotic adjustment would be a successful mechanism for these plants to acclimate to summer drought. If osmotic adjustment occurred, then stomatal conductance would increase, placing additional demands for water flow on the vascular system. As a result, the tension in the vascular system would increase and there would be a higher chance for drought induced embolism.

Few studies have been done on the vulnerability to drought induced embolism in Rhododendron species. The water potential that caused 50% loss of hydraulic conductivity for GR was between -2.42 and -3.1 MPa depending on the technique used (Cordero and Nilsen 2002). Therefore, GR is relatively vulnerable to drought induced embolism. Other Rhododendron species may be slightly more tolerant of drought induced embolism. For example, the water potential that induced 50% loss of hydraulic conductivity was between -2.96 and -3.5 MPa for R. macrophyllum in the Oregon Cascade mountains (Cordero and Nilsen 2002).

4.4. Nutrient use

Rhododendron species typically inhabit acid soils with relatively low nutrient availability. In accordance, leaf tissue nutrition is representative of a sclerophyllous plant. For example, tissue nitrogen concentration of GR leaves range from a high of 1.25% when juvenile to a low of 0.25% upon abscission (Nilsen, pers. data). The low tissue nitrogen concentration of GR leaves is reflected in the low (2-7 moles m⁻² s⁻¹) average leaf photosynthetic rate (Bao and Nilsen 1988, Lipscomb and Nilsen 1990a, Nilsen 1992). Evergreen plants of low nutrient regions tend to recycle nutrients effectively (Chapin 1980) and Rhododendron species are no exception. This is supported by the low nutrient content in leaves when they fall and by their slow decomposition rate. Due to the light nutrient recycling and the calcifuge litter, soils below Rhododendron thickets can become depleted in certain nutrients (Nilsen et al. 2001, Beier et al. 2005). In fact, GR retains a large portion of available cations in its leaf mass in Southern Appalachian forests (Monk et al. 1985).

Mycorrhize (beneficial fungal associates with plant roots) are important for plant nutrition of most forest species. Species of Rhododendron harbor a specific form of fungal associate termed “ericoid mycorrhize”. These fungal associates tend to inhabit the undecomposed litter of the forest floor. Therefore, Rhododendron species have root associates that are the earliest to acquire nutrients from decomposing leaf tissues on the forest floor. There is evidence that GR thickets inhibit the symbiotic association of mycorrhize on the roots of competing species (Walker et al. 1999). The ericoid mycorrhize, and the inhibition of mycorrhize association on other plants increase the ability of GR to compete for limiting nutrients in upper soil layers.
4.5. Allelopathy

Many species of *Rhododendron* contain allelochemicals (probably to minimize herbivore damage of leaves) that are utilized by indigenous people for medicinal purposes. For example, an aqueous soloution made from leaves of *R. dabanshanense* is successfully used for treatment of bronchitis in China and this extraction contains multiple phenolic compounds (Yang and Wang 1978, Wang and Yang 1981). Water soluble phenolic compounds are long known to have allelopathic potential (Rice 1979). Therefore, decomposition of abscised leaves or leaching chemicals out of leaves by precipitation may release potentially toxic compounds into the soil. The allelopathic action of these compounds on other species is confined by the climate, soil chemistry and soil microbes. In one study of GR, toxicity of aqueous leaf extracts could be demonstrated for root elongation of a bioassay species, but no toxicity could be demonstrated for native species in the lab or the field (Nilsen et al. 1999). In contrast, studies of PFR have demonstrated the presence of phenolics in leaf extracts and strong inhibition of *Festuca ovina* (a common grass) growth (Rotherham and Read 1988). Therefore, there is potential for allelopathic inhibition of associated species by leachates from Rhododendron species or decomposing parts of Rhododendron species. The efficacy of Rhododendron allelopathy can not be generalized and must be evaluated for each individual combination of Rhododendron species, climate, soil and associated species.

4.6. Primary plant strategy

The ability of plants to allocate resources among different organs and functions can directly account for their survival (Radosevich et al. 1997). Radosevich et al. (1997) reported that various theories have been developed to explain ‘the patterns of resource allocation’ in plants. These theories include the *K*- and *r*-selection theory (MacArthur 1962) and the *C*- and *S* selection by Grime (1979).

Plants are arranged on a scale between two distinct ends of resource allocation in the *r* and *K* selection theory (Radosevich et al. 1997). The main feature of *r*-selected plants is ‘productivity’. *R*-selected species are characteristic of ‘variable and/or unpredictable’ environments (e.g. open sites and early successional sites) and *r*-selected species have relatively short-life spans. *R*-selected plants allocate a large fraction of photosynthetic resources to regeneration (Radosevich et al. 1997). Extended life-span, long pre-reproductive period and a small fraction of resources allocated to reproduction are among the traits of the ‘*K*-selected’ species. *K*-selected species are characterized by their ability to dominate environments and in the late stages of the plant succession. The pattern of resource allocation for this type of plant is based on ‘efficiency’ (Radosevich et al. 1997).

Grime’s *C*, *R*, and *S* selection theory expands on the previous theory (Grime 1979). The theory focuses on two site factors, ‘stress and disturbance’. Four potential strategic scenarios, dictated by the low and high levels of stress and disturbance, were described. Plants are defined as ‘ruderals (R), stress tolerators (S), or competitors (C)’ based on this theory. Ruderal and stress tolerators correspond to the *r* and *K* strategy (Radosevich et al. 1997).

Radosevich et al. (1997) categorized many trees and shrubs as ‘stress-tolerant competitors’ (CS). Invasive plants grow quickly, have high reproductive output, often have vegetative reproduction and are highly competitive (Baker 1974, Erfmeier and Bruelheide 2004). These plants are characterized by rapid biomass production and vigorous height and foliage growth. Physiological, morphological, and behavioral plasticity are important for invasive species in light-limited environments (Radosevich et al. 1997, Niinemets et al. 2003).

CS-selected plants primarily invade an area by seed after a disturbance. Although vegetative growth rate is not present in the seedling stage, it accelerates profoundly following maturity. Physical disturbance often triggers prolific vegetative reproduction in invasive plants (Radosevich et al. 1997). Rhododendron species often fit the CS-selected definition according to the results of numerous past studies (Gritten 1995, Mejias et al. 2002, Niinemets et al. 2003, Nilsen and Horton 2003, Erfmeier and Bruelheide 2004).

Many successful invasive plants display duplicity in reproduction (Radosevich et al. 1997). Under stable environments, ‘inbreeding’ predominates, which preserves the genetic combinations that proved to be successful in previous colonization. ‘Outcrossing’ predominates when invasive plants are faced with new or dynamic environmental conditions (Radosevich et al. 1997). Rhododendron species display similar duplicity in different locations and specific environments (Erfmeier and Bruelheide 2004 2005). PFR primarily reproduce by vegetative means (i.e. branch-layering) in Georgia and Spain where it is not invasive and in Turkey where it is considered greatly problematic. In light-limiting environments, seed set is inhibited and seed germination is limited because there are few ‘safe sites’. On the other hand, PFR regenerates in Ireland mainly by seed (Cross 1981, Mejias et al. 2002, Erfmeier and Bruelheide 2004) and hybridizes with other Rhododendron species (Milne and Abbott 2000, Chamberlain 2003, Niinemets et al. 2003, Rotherham 2003). Abundant ‘safe sites’ coupled with high seed production (50,000 seeds per flower, Mabbett 2005) due to the fact that high solar radiation promotes vigorous flowering (150 flowers m⁻², Mejias et al. 2002) increase the likelihood that seedlings will survive. Consequently, Erfmeier and Bruelheide (2005) reported that the Irish populations reflect ruderal and competitive characteristics of Grime’s theory whereas the stable populations of PFR in Georgia and Spain populations reflect stress tolerant selection. However, Turkish populations of PFR do not follow either strategic pattern of Erfmeier and Bruelheide (2005) because the PFR in Turkey has both strong stress tolerance and high invasiveness. Therefore, Radosevich’s competitive stress tolerator (CS) term might be more suitable for the Turkish PFR populations.

Mechanisms of succession may help us understand the competitive success of Rhododendron species (Radosevich et al. 1997). There are several models for succession. For example, the ‘facilitation, tolerance, and inhibition’ models of Connell and Slatyer (1977) and the ‘resource-ratio’ model of Tilman (1985) are two well-supported models for succession. Of these, the tolerance and resource-ratio models may best describe the behavior of Rhododendron species in succession. According to the ‘tolerance’ model, succession is mainly driven by the abilities of species to harvest site resources that progressively become limiting as succession proceeds (Radosevich et al. 1997). The resource-ratio model assumes that each species is a specialist for acquiring a narrowly defined part of scarce resources (Radosevich et al. 1997). The relative availability of scarce resources progressively declines over time as the community grows. Therefore, the species with the lowest combined resource requirement will outcompete the other species over time. Hence, a decrease in the most limiting resource or condition brings about domination by the species that require the least resources. In this model, competition energizes succession (Radosevich et al. 1997). The ecophysiological characters of Rhododendron species that include high resource use efficiency and extremely high shade-tolerance are the mechanisms by which Rhododendron dominates a resource-ratio based succession.
5. CONTROL OF RHODODENDRON

Most woody eradication efforts are inconclusive, due to Rhododendron's amazing capability to counteract most control technologies (Lawrie and Clay 1993). In addition to prevention, various woody control methods have been used against Rhododendron including manual (cutting and uprooting), mechanical removal, burning, biological control, and chemical control. Controlling PFR populations imposes a great financial burden in Turkey and the UK (E en and Zedaker 2004, Willoughby et al. 2004). There is a significant variation in the cost of controlling Rhododendron populations in the literature, due to differences in human population density, local economies, regional labor-rates and topography. Partial control of one hectare of PFR varies between €150-1,000 in the BSR of Turkey (E en, personal data) whereas total woody control of PFR ranges between €60-10,300 for the UK, depending on PFR density and the method of control used (Willoughby et al. 2004). Research is underway in Turkey to assess the potential, cost-effective use of PFR in the wood industry to lower the cost of PFR control.

5.1. Prevention

Rhododendron is a very good example of weeds that can successfully use either predominantly generative or predominantly vegetative reproduction in different environments (Erfmeier and Bruehlheide 2004). Seed is the major colonization process for Rhododendron in Ireland and UK whereas vegetative reproduction predominates colonization of disturbed sites in the BSR of Turkey (Saatçılu 1957, Rotherham 2003, Erfmeier and Bruehlheide 2004). In both cases, disturbance provokes prolific population expansion of this woody weed. Thus, avoiding unnecessary disturbance on sites that are potentially prone to Rhododendron invasion is an important prevention consideration (Tabbush and Williamson 1987, Mabbett 2005).

Approaches to prevention should vary along with the major colonization strategy of the invader. PFR generally grows in pockets of thickets in the UK and colonizes new sites by seed. Moss populations up to 1-cm in depth provide safe sites for PFR seed germination. Activities that disturb the soil such as grazing and forest management practices coupled with high moisture promote moss development and results in PFR stand expansion. One PFR shrub can shed as many as 1.5 million seeds that are easily distributed by wind because of their small size. Eradication of major seed sources along the most common wind direction, minimizing soil disturbance and reducing moss formation on uninundated sites might be an effective, short-term prevention approach in places where seed is the main reproduction strategy. After that is accomplished, control efforts should be focused on younger bushes that have rapid growth and high reproductive rates (Tabbush and Williamson 1987, Gritten 1995, Rotherham 2003, Edwards 2005, pers. comm., Gritten 2005, pers. comm., Mabbett 2005).

The Northern Anatolian Mountains of the BSR is a rough, highly heterogeneous local with many different microclimates. Slopes in the region are generally greater than 20% (Atalay 1992). Aside from human settlements, these rural slopes contain either relatively closed forest canopies or forest fractured by islands of agricultural land. The region's macroclimate is generally less humid than that of the British Isles. Thus, there is relatively less room for bryophyte establishment when compared to the British Isles. Branch layering is the primary invasion means of PFR in the Northern Anatolian Mountains of the BSR (Tabbush and Williamson 1987, Çolak 1997). Vegetative expansion is often triggered by disturbance, which activates the dormant adventitious buds of PFR (Tabbush and Williamson 1987, Çolak 1997, Mabbett 2005). Regulation of fire-wood utilization of PFR-dominated sites by the local communities as well as regulation and careful planning of forest operations on those sites can provide short-term solutions to the PFR problem in the region (Çolak 1997).

Relaxing strict fire-exclusion policy in the region, may be considered another long-term solution. Preserving native plant cover such as bramble (Rubus fruticosus L.) or grass may significantly curb PFR invasion onto new sites (E en 2000, Tonbridge 2002, Rotherham 2003). Herbaceous weed control might be delayed in forest regeneration areas that are likely to be invaded by PFR, and both herbaceous and woody weed control might be carried out accordingly at the time of regeneration (E en 2000).

Shade is another silvicultural tool to control PFR populations. Establishing a dense canopy primarily made up of conifers including western hemlock (Tsuga heterophylla), yew (Taxus spp.), fir (Abies spp.), and spruce (Picea spp.) may control PFR in the understory (E en 2000, E en et al. 2004, Willoughby et al. 2004). Abundant conifers in the overstory of the BSR forest during the Ottoman Period (Kutluk 1948) may have controlled PFR, when compared to the present pure beech forests of today (E en et al. 2004).

5.2. Manual control

As the most traditional weed control method of the world's cultivation, manual control has been and is still being employed against invasive plant species around the world (Radosevich et al. 1997). Manual PFR removal is carried out either in a broadcast manner or in bands (Tabbush and Williamson 1987). Removal of PFR in strips that are nearly twice as wide as the mean PFR population (e.g. 4m) and piling the removed stems on the top side of the cut bands is a common manual method employed in both Turkey and the UK (Fig. 1D). This method is preferred because it is cost effective and maximizes soil and nutrient conservation (Tabbush and Williamson 1987, Atay 1990, E en 2000). Various tools including hand sickles, hatchets, and machetes are traditionally used to cut PFR. Hand-cutting stems nearly 10 cm above the ground is still commonly used for PFR suppression by the Turkish Forest Service in the BSR (E en and Zedaker 2004) and in the British Isles (Dehnen-Schmutz et al. 2004, Willoughby et al. 2004). Burried pieces of root and stem left in the soil after a manual cut coupled with the facility for root and stem suckers by PFR after a disturbance make cutting ineffective (Tabbush and Williamson 1987, Palmer et al. 1988): In a recent Turkish study, cutting caused approximately 20% reduction in the mean basal area of PFR two and five years after treatment (YAT), as compared to non-woody-control treatment (E en and Zedaker 2004, Kulac 2004). High cost is another limiting factor for manual control (E en and Zedaker 2004). PFR control (mostly manually) in the 2,173 km 2 sampled area of Snowdonia National Park of North Whales, UK, cost more than €66 million, making the unit cost around €304 ha⁻¹ (Gritten 1995). The cost of manual control coupled with burning ranges from €3,500 to 16,000 in the UK (Willoughby et al. 2004). In a recent Turkish study, the cost of broadcast manual cutting of one hectare of Rhododendron was reported to vary between €200-1000, depending upon wood density and topography (E en, pers. data). The cost effectivity (cutting cost ha⁻¹ divided by percent stump basal area control ha⁻¹) of cutting was 30-fold greater, as compared to the most cost-effective treatment in the same study (E en and Zedaker 2004). Moreover, the recent decline in available labor for manual control, due to the low labor-rate also makes manual woody control
unattractive (Huss 1991, Çetinta 2000, pers. comm.).

Uprooting is another common practice in PFR control (Çolak 1997, E en and Zedaker 2004, Willoughby et al. 2004). This particular manual treatment has a clear superiority over cutting in control and cost-efficacy (Figs. 1E, 1F). Rhododendron roots are seldom deeper than 45 cm in the soil and are mostly distributed in the litter, humus, and the upper horizons (Çolak 1997). Since Rhododendron's root system mostly grows uphill, uprooting them from upslope is relatively easy (Çolak 1997, E en and Zedaker 2004). Uprooting controlled PFR nearly 5- and 15-times more after two and five YAT, respectively than did cutting (E en and Zedaker 2004, Kulaç 2004, respectively). Although uprooting and cutting have similar per-ha cost (€260-796, E en, pers. data), uprooting had a 26-fold greater cost-effectiveness after two YAT, as compared to that of cutting. However, similarly to cutting, use of uprooting for PFR control will probably suffer from the declining labor-force in the near future (E en and Zedaker 2004).

Removing PFR from treatment bands by uprooting or cutting and piling the woody debris in the next buffer band apparently improves habitat for rodents and may increase predation of planted and naturally seeded tree seedlings. Increased herbivory has been observed for beech and oak seedlings growing in PFR and GR populations, respectively (Çetinta 2000, pers. comm., E en 2000, Lei et al. 2002).

5.3. Mechanical control

Brush raking, brush lading, winching, excavating, and chopping are commonly used with machinery to remove PFR in the British Isles (Tabbush and Williamson 1987, Murgatroyd 1996 1998, Dehnen-Schmutz et al. 2004, Willoughby et al. 2004). Since mechanical removal prepares the site for forest regeneration, and enhances short-term silvicultural goals (minimize loss of nutrients and enhance seedling establishment by natural regeneration) this technique has gained popularity in Turkish forest management. For instance, the rate of beech natural regeneration was 2.5-fold greater with mechanical removal when compared to hand-pulling one YAT (Sargınç 2005). Mechanical removal of PFR is not preferred in other parts of the world, because of rapid site re-invasion from buried stem and root parts, re-seeding from nearby populations, limited effectiveness of machinery on heterogeneous topography such as the BSR and concerns for soil and site productivity (Wood et al. 1967, Tabbush and Williamson 1987, E en 2000, Willoughby et al. 2004).

Large operational costs are reported for mechanical control of PFR. Murgatroyd (1996 1998) stated that excavators with flails could not operate on wet slopes greater than 45-50° in western Scotland and the relevant cost ranged between £700-8,000. Similar to manual control, mechanical woody removal can be implemented as either broadcast or partial control (Sargınç 2005). Clearing bands 40-60 m apart by bulldozers costs €250 ha⁻¹ in the UK (Fig. 1G). Further passes by bulldozers within the next four years to prevent reinvasion of the bands by PFR added €118 to the previous figure, totaling €368 ha⁻¹ (Robinson 1980).

Mechanical removal leads to concerns for long-term site productivity, especially nutrient poor soils (Childs et al. 1989, Rotherham 2003, Willoughby et al. 2004). Heavy traffic on forest soils by mechanical equipment compacts the soil, diminishes macroporosity and organic matter, causes rutting and puddling of mesic or waterlogged soils, enhances sedimentation and nutrient leaching rate, and causes nutrient pollution in streams (Childs et al. 1989, Willoughby et al. 2004). Taken as a whole, this method reduces long term forest tree growth (Childs et al. 1989). Additionally, the discharge of environmental pollutants from the machinery threatens the local flora and fauna (Johnston and Nickerson 1991, Willoughby et al. 2004). A recent Turkish study of the effects of various PFR control methods on long-term site productivity found that woody control with heavy machinery reduced soil organic matter, nitrogen, phosphorus, calcium, potassium, sulfur, and magnesium by 75-91% one YAT when compared to those in hand-pulled site. Mechanical removal also reduced soil cation exchange capacity by half. Nutrient leachates from the mechanical control site were great, varying between 14-219-fold that of the hand-pulled site (Sargınç 2005).

5.4. Burning

PFR control by burning is cost-efficient, easy, and rapid compared with other methods (Romancier 1971). Burning alone is not effective on both PFR and GR and yields more vigorous re-growth than other techniques. Repeated low-intensity burns can exhaust food reserves in PFR roots and reduce the density of PFR significantly over time (Shaw 1984, Çolak 1997). Although re-growth of PFR occurs in the same growth period as cutting takes place (E en 2000), regrowth occurs in the second year after burning (Atay 1990). Burning is commonly employed in the British Isles not as a control, but as a method of disposing stems after cutting (Dehnen-Schmutz et al. 2004, Willoughby et al. 2004).

Hardwood-dominated forests such as beech forests of the BSR are very fire-sensitive (Çolak 1997, E en 1992) discussed the potential of using biological control application (Radosevich et al. 1997). Biological control (biocontrol) can be an effective, cost-effective, and easy technique. This method is favored when other weed control methods are ineffective or inoperable, the value of land has fallen, and there is a low risk of off-target damage in the vicinity of biological control application (Radosevich et al. 1997).

Use of biocontrol on Rhododendron species is still under development (Evans 2003). Holden et al. (1992) discussed the potential of using biological vectors to control PFR. Evans (2003) evaluated two different approaches to biocontrol (traditional and inundative). The traditional approach uses non-native biocontrol species whereas the traditional approach uses native biocontrol species. Using an exotic pest to control Rhododendron population is not preferred in the UK, due to numerous other ornamental, non-invasive Rhododendron species in gardens that might suffer off-target damage (Evans 2003). However, exotic pests may have some potential for use in the BSR of Turkey.

Mycocerbicides have been used in the UK inundatively, to control unwanted vegetation in the same way that conventional herbicides are
applied (Radosevich et al. 1997). Currently, a mycoherbicide from Chondrostereum purpureum (Pers.), a pathogen naturally occurring on various hardwood species in the BSR of Turkey, is being evaluated against PFR in the UK (Evans 2003). This mycoherbicide was found to be as effective on red alder (Alnus rubra) as an efficacious herbicide (glyphosate) in Canada (Becker et al. 2005). Furthermore, a newly emerging pathogen (Cryptosporiopsis sp.) is under investigation for potential use in Rhododendron control (Seiser and Evans 2003).

The bioherbicide approach has certain superiorities over the traditional approach. Using native species as a bioherbicide saves difficult, long importation requirements. Careful application of the bioherbicide can control the pathogen’s population minimizing off-target-damage (Evans 2003, Green 2003).

5.6. Chemical control

Forest resources have become more intensively managed because of the increasing global gap between demand for and supply of wood resources. Herbicides constitute a major part of this management intensification. In fact, herbicides are extensively used to improve forest growth and yield around the world (Guynn et al. 2004). Herbicides improve wood harvest volume over the long-term by 50-150% in the North American forests when applied to young stands (Guynn et al. 2004, Wagner et al. 2004).

Herbicides are largely used against Rhododendron around the world either alone or coupled with manual control methods. Herbicides are selected for other methods because of rapid and long-term efficacy and high cost-effectiveness ($100-160) (Tabbush and Williamson 1987, Rotherham et al. 2003, Dehnen-Schmutz et al. 2004, E en and Zedaker 2004, Willoughby et al. 2004). Different application techniques including foliar, basal, cut-stump, and stem-injection chemical are available for Rhododendron control (Tabbush and Williamson 1987). Plant population density, distribution, and height, as well as economic (e.g. labor-rates) and social factors (e.g. public perception) determine the preferred chemical technique Rhododendron control in a specific geographic setting (Britt et al. 2003).

However, there is a growing tendency to steer away from herbicides around the world (Radosevich et al. 1997, Guynn et al. 2004). Damage to non-target organisms, soil and water pollution, human health and safety issues, and habitat change cause many concerns about applying herbicides in forest management programs. More strict regulations are being put in place for the use of herbicides at both national and international levels.

Nonetheless, numerous past studies on herbicides and their effects in the environment have established that most of these concerns about herbicide arise from a lack of information. The modes of herbivore action and interaction of herbicides with insects and fungicides (Radosevich et al. 1997, Guynn et al. 2004) are poorly understood. Herbicides are not toxic to non-target organisms when used at recommended application doses. Herbicide modes of action are specific to plant metabolism (e.g. photosynthesis) and are not likely to affect other organisms. Recently developed compounds do not have residual activity in the environment and to not accumulate along the food chain. Also, potential risks can be reduced further by appropriate choice and use of herbicide, application method and timing, correct handling and appropriate transportation conditions (Radosevich et al. 1997, Guynn et al. 2004).

5.6.1. Directed foliar control

Chemical compounds can be applied directly onto the foliage of the target species, using knapsack sprayers (Zedaker 1988, Smith et al. 1997, Britt et al. 2003). PFR is hard to kill even with herbicides (Laurie and Clay 1993). Repeated herbicide applications with low rates may effectively control this shrub species. 2, 4-D mixtures, ammonium sulphamate, dicamba, glyphosate, imazapyr, and triclopyr herbicides, most of which have common uses for site preparation, herbaceous and woody weed control, and conifer release, are employed against PFR (Monaco et al. 2002, Britt et al. 2003, Willoughby et al. 2004). Direct foliar application has clear advantages over others for long-term, effective, cost-efficient Rhododendron control in settings where PFR populations either are young seedlings or are tall (<6-m), and dense (8,000 stems ha⁻¹) with slim stems (<5-cm) (Zedaker 1986, Willoughby et al. 2004, Figs. 1H, 1I). In tall (2-5-m), dense (48,000-90,000 stems ha⁻¹) PFR populations, foliar herbicides yielded at least twice as much wood control as did cutting and cut-stump spray applications 2YAT. Foliar treatments on average had eight-fold greater cost-effectiveness, when compared with cut-stump treatments (E en and Zedaker 2004). Also, the greater efficacy of this technique continued into the fifth year of the study (Kulaç 2004, E en et al. 2006a).

A sufficient amount of leaf absorption and translocation in the plant are key factors to the success of direct foliar application. PFR foliage has a complex, rich waxy layer. The hydrophobicity of the waxy epicuticular layer on the adaxial leaf surface forms a significant barrier to herbicide penetration into the leaf interior. However, herbicides with a lipophilic base can circumvent this problem (Tabbush et al. 1986, Gritten 1995, Rankin 2003). Photosynthetic activity enhances herbicide translocation. PFR has active photosynthesis year-round, but photosynthesis is limited in GR during the fall and winter. Thus, there is a wide time-frame for the application of the symplastically active herbicides on PFR. However, it is recommended to apply herbicides between mid-July to mid-September, when the major translocation route is downward (source-to-sink). Herbicides including 2, 4-D, glyphosate, imazapyr, and triclopyr ester mostly accumulate in the roots during this time (Robinson 1980, Tabbush and Williamson 1987, Radosevich et al. 1997).

Triclopyr ester (Garlon 4) is a synthetic, oil-soluble, symplastically translocated, auxin-type, growth regulator herbicide that diffuses and penetrates hydrophobic plant surfaces (Monaco et al. 2002). In a herbicide uptake and translocation study on GR, triclopyr ester had more than 95% of its total activity absorbed by foliage 72 hours after treatment, which was 60% greater than imazapyr’s total leaf absorption (E en et al. 2006b). Triclopyr ester has low toxicity on animals and low residual activity in the soil (Smith et al. 1997).

Imazapyr (Arsenal, Arsenal 50) is another systemic herbicide with a broad spectrum of control on many herbaceous and woody weeds (Monaco et al. 2002, Britt et al. 2003). Although its leaf uptake is significantly less than triclopyr ester, it is readily translocated within Rhododendron to the main target (i.e., roots). In the aforementioned GR study, imazapyr had almost twice as much activity translocated to the roots of GR, when compared to triclopyr ester (E en et al. 2006b). Sunflower seed oil surfactant can improve leaf absorption of imazapyr and bring it up to the leaf uptake level of triclopyr ester. These results help to understand the physicochemical mechanism behind the superior performance of imazapyr (the rate of 5-10% v:v or 3-6 kg ha⁻¹) in PFR control in the BSR, when compared to triclopyr ester (the rate of 2.5-5% v:v or 2.6-5.1 kg e⁻¹; E en and Zedaker 2004). Most conifer seedlings tolerate this herbicide year-round. Thus, imazapyr can effectively be used in conifer stands such as spruces (Smith et al. 1997). Imazapyr arrests “acetoxyhydroxacetid synthase” and prevents valine, leucine, and isoleucine synthesis, which are fundamental amino acids for protein synthesis and cell division in meristematic tissues. Exhaustion of proteins in
plants takes time; therefore, in contrast to triclopyr, imazapyr becomes effective after an extended period (Smith et al. 1997). For example, triclopyr ester had control effects as early as 10 days after application, but defoliation of imazapyr treatments occurred two YAT (E en 2000). Imazapyr has high residual activity in the soil (Smith et al. 1997).

Glyphosate is another post-emergence, non-selective powerful foliar chemical for eliminating a broad spectrum of herbaceous species and woody weeds. Similar to imazapyr and triclopyr, glyphosate is an herbicide that translocates from the foliage to the roots. It interferes with amino acid and protein synthesis in the plant. Selectivity can be achieved by directed foliar application with this herbicide. Glyphosate is widely used for conifer release in the US before conifers start meristematic activity. Glyphosate is synergistic with imazapyr in woody control (Smith et al. 1997, Monaco et al. 2002). Such mixtures should be tested in Rhododendron control to reduce herbicide volume discharged to the environment, to enhance environmental safety and to increase cost-efficacy. Although not as effective in Rhododendron control as imazapyr and triclopyr, glyphosate is used more often for PFR control than the latter two herbicides. This is probably due to its relatively low risk for human health and safety, its lower residual activity in the soil and its low product cost (Tabbush and Williamson 1987, Lawrie and Clay 1993, Smith et al. 1997).

2,4-D is a symplastically-translocated, auxin-type, growth regulator, phenoxy herbicide, commonly used for conifer release, site preparation purposes, and controlling broad-leaved herbaceous vegetation in grasses, woody weeds in forests and aquatic weeds (Ross and Lembi 1989). It is mobile in the phloem. In addition, it is much less phytotoxic and less mobile in plants, compared to its chemical relative triclopyr ester. 2, 4-D has lost its popularity since the emergence of modern herbicides (Smith et al. 1997). If used, 2,4-D is mixed with other herbicides including dicamba and triclopyr ester for application on PFR (Willoughby et al. 2004).

Ammonium sulphamate (AMS) is a systemic, inorganic herbicide. It is a non-selective, post-emergent compound with low soil residual activity and relatively high environmental and mammalian safety. It replaces 2,4-D where there are environmental concerns (Ross and Lembi 1985, Monaco et al. 2002, Britt et al. 2003).

Surfactants (surface active agents) that are added to herbicide spray solutions can also circumvent the leaf barrier and improve Rhododendron control. These compounds reduce the surface tension of spray deposited on leaves, resulting in greater transformation from the aqueous/air interface to the liquid/solid interface. Surfactants lead to enhanced spray retention on leaves, increased spreading on leaf surfaces, and increased penetration into leaves, which in turn enhances herbicide uptake by plants (Tabbush et al. 1986, Zedaker et al. 1994, Jackson et al. 1995 1998). Adding surfactants including seed oils such as sunflower and non-ionic surfactants such as Mixture®B to herbicides solutions have become conventional in Rhododendron control (Tabbush et al. 1986, E en et al. 2006b). A sunflower-seed-oil-based surfactant added to imazapyr at 25% (v:v) rate improved total leaf uptake and translocation to roots by at least 75 and 53%, respectively, when compared to non-ionic and organosilicone surfactants. Therefore, vegetable oils are recommended to improve imazapyr’s poor leaf uptake and in turn further improve its mobility in the plant (E en et al. 2006b).

Costs of foliar applications vary. Spraying triclopyr onto PFR costs between €221-361 in Turkey (E en pers. data) whereas foliar or cut-stump treatment costs vary between €264 and €882 ha⁻¹ in the UK (Willoughby et al. 2004). Applying imazapyr onto PFR foliage in the BSR ranges between €450-800 ha⁻¹. Glyphosate is a more cost-effective herbicide than the other herbicides with costs (foliar or cut-stump) ranging from €70 to €370 ha⁻¹ (Willoughby et al. 2004).

5.6.2. Stem injections

This technique is most productive when applied on stems with diameter between 5 and 30 cm. In this technique, the cambium layer of Rhododendron bark is wounded with a conventional hand axe and compounds (in pure or diluted form) are immediately injected into the wound using a squirt bottle. This technique is commonly called the "hack-and-squirt technique". Recently, modern tools such as small, light-weighed 'hypo-hatchets' are used for stem injections of PFR. Hypo-hatchets automatically inject a calibrated amount of compound simultaneously with wounding. This technique in general consumes about 325-500 ml of herbicide per m 'hypo-hatchets' are used for stem injections of PFR. Hypo-hatchets commonly called the 'hack-and-squirt technique'. Recently, modern tools such as small, light-weighed 'hypo-hatchets' are used for stem injections of PFR. Hypo-hatchets automatically inject a calibrated amount of compound simultaneously with wounding. This technique in general consumes about 325-500 ml of herbicide per m² around the trunk, one to two ml of chemical is applied into each wound. Equidistant placement of wounds around the trunk is critical (Zedaker 1988, Britt et al. 2003, Willoughby et al. 2004).

5.6.3. Cut-stump spray

Painting or spraying the cambium of cut stem surfaces of arboreous weeds with undiluted or water/oildiluted herbicides is a successful weed control technique that may prevent PFR from sprouting. When applied properly, the cut-stump's low use rates (260-300 ml m⁻² basal area) make this technique more environmentally safe and cost-effective than the other herbicide techniques. Since placement primarily determines herbicide selectivity, targeting the phloem conduits by which compounds move to the site of action is critical. In general, this technique is most effective when herbicide is placed on stumps 30 cm diameter. Targeting the cambial surface is difficult on thinner stems, resulting in greater chemical wastage, higher environmental risks, poor cost-effacy and poor control efficacy (Zedaker 1988). This was the case for cut-stump herbicide control of the PFR in Turkey where there were dense populations with thin stems (E en and Zedaker 2004, E en et al. 2004 2006a). Cut-stump treatments conferred an intermediate reduction in mean basal area between foliar treatments (approx. 50% less) and cutting (approximately three times greater, E en and Zedaker 2004, E en et al. 2006a). Also this treatment was relatively expensive (€480-1150 ha⁻¹; E en pers. data). Cut-stump spray is however a common and effective means of woody control where Rhododendrons form populations with less density and thicker stems (Zedaker 1988).

5.6.4. Devising a feasible integrated approach

Integrated weed control is an important part of woody weed management. Many factors determine the type and sequence of different weed control methods chosen for a given weed problem (Ross and Lembi 1985, Radosvich et al. 1997). Some of the factors are the abundance, distribution, population structure and ecology of the weed species. Moreover, ecological constraints of a given site (e.g. sensitivity of the soil/site to factors that degrade long-term productivity), the type of management agenda, operational and financial capabilities of the landownership, and the legal and public perception regarding a particular woody control technique are important. An integrated management policy is built upon understanding these and other factors concerning control of the invasive species.
When an active intervention is needed on a given site, an integrated management program is devised by first identifying and then properly arranging the viable woody control techniques in relation to the ecological limitations of the site, financial factors and feasibility of woody control. For instance, the high PFR population density in the BSR prohibits cut-stump treatments. Therefore, manual (uprooting), foliar herbicidal, and mechanical control are left as viable alternatives (E en et al. 2004, E en et al. 2006a). Mechanical scarification of the top soil by bulldozers may seem the most desirable control technique provided that heavy machinery can be used. The Turkish Forest Service has recently used this technique. Speed, practicality, cost-efficiency and a rapid and high-rate of natural canopy tree seedling establishment make mechanical treatment practical in the BSR (Sargıncı 2005). The disadvantages of using heavy machinery for long-term soil productivity including soil compaction, rutting and nutrient leaching can be alleviated by making some adjustments on the application protocol. Using tires instead of tracks on the machinery is one of them (Childs et al. 1989). Also, mounting rakes with teeth that are widely spaced allows the operator to sieve top soil through the teeth and remove Rhododendron’s root system (Sargıncı 2005).

The effects of weed control on long term site productivity and tree growth response have been established (Yıldız 1997, Ballard 2000). In a Douglas-fir (Pseudotsuga menziesii Mirb.) study in coastal Oregon of the US, partial vegetation removal (50%) secured substantial seedling establishment. The mean relative growth rate of 15-year old Douglas fir trees growing on the partial control site did not significantly differ from that of trees growing on the complete control site (Yıldız 1997). Hence, scarifying Rhododendron on 40-60 m bands leaving buffer bands where woody stems are not removed may be an alternative in cases where long-term soil productivity is a concern (Robinson 1980). These buffer zones not only prevent soil erosion and organic matter loss but also serve as a ‘sink’ for nutrients made available after disturbance on the nearby treatment sites. After the roots of the seedlings of crop trees or desired native vegetation are large enough to capture nutrients available in the soil solution, the untreated Rhododendron behind can be removed. Because of these long-term productivity and cost-efficiency advantages, partial Rhododendron control instead of complete removal should always be desired no matter which control technique is chosen (Kulaç 2004, Sargıncı 2005).

Numerous alternative control techniques and sequences can be devised in an integrated approach under various circumstances. For the sites where soil erosion or/and long-term productivity are major concerns, cutting or uprooting woody stems followed by the foliar herbicidal treatment of sprouts or new seedlings may constitute a desirable integrated approach. When the woody weed density is low or when the weeds grows in patches, cutting may be the best vegetation control technique. Controlling woody density with foliar herbicides and burning dead material (Dehnen-Schmutz 2004) may be the best technique when the woody weed has a uniform and dense coverage. However, this specific approach is not possible for sites where fire-sensitive tree species (e.g. beech) are grown and fire-exclusion policy is strictly enforced, as in mesic Turkish BSR forests.

6. EFFECTS OF REMOVAL ON ECOSYSTEM PRODUCTIVITY AND COMPETITION

After forest disturbance, disturbance-resistant species can dominate a site for years before canopy closure. Rapid site colonization by Rhododendron may delay the establishment of economically desirable target species because of competition for sunlight, moisture, and nutrients. Yıldız (2000) demonstrated that complete weed removal for the first five years of stand development increased Douglas fir biomass after 15 years by about 450% relative to no vegetation control sites in the Coast Range of Oregon. Thus, during stand initiation stage, tree seedlings need to be released from competition with Rhododendron until seedlings overtop shrubs.

However, intensive removal of competing species from sites may disturb the ecological integrity of forest ecosystems. Decision about retaining or removing an understory weed population depends upon understanding the balance between the understory’s detrimental effect on competition and its beneficial effects on soil fertility.

Ecosystem productivity and nutrient retention generally increase with an increase in species diversity (Tilman 1987). Different adaptations among species in a diverse site result in a more complete use of site’s resources. For example, the differences among species rooting depths and in patterns of absorption of mineral nutrients may result in complete use of nutrients and water (Perry 1994, Yıldız 2000, Kozłowski 2003).

Soil organic matter has a major influence on soil structure, water retention and nutrient reserves. Substantial amounts of soil nutrients, such as N, P, Ca and S are incorporated into soil organic matter (Stevenson 1986, Wild 1988). In a recent study, forest floor organic matter under eastern beech forest with an understory of PFR was found to contain about 32 kg ha\(^{-1}\) of N, P, Ca and S as are incorporated into soil organic matter (Stevenson 1986, Wild 1988). Mechanical scarification of the top soil by bulldozers may seem the most desirable control technique provided that heavy machinery can be used. The Turkish Forest Service has recently used this technique. Speed, practicality, cost-efficiency and a rapid and high-rate of natural canopy tree seedling establishment make mechanical treatment practical in the BSR (Sargıncı 2005). The disadvantages of using heavy machinery for long-term soil productivity including soil compaction, rutting and nutrient leaching can be alleviated by making some adjustments on the application protocol. Using tires instead of tracks on the machinery is one of them (Childs et al. 1989). Also, mounting rakes with teeth that are widely spaced allows the operator to sieve top soil through the teeth and remove Rhododendron’s root system (Sargıncı 2005).

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occupied soils. The low availability of P and the inhibition of mycorrhizal colonization make it likely that the presence of Rhododendron reduces the availability of canopy tree seedlings to compete for soil nutrients. In nutrient deficient soils, Rhododendrons with mycorrhizal roots effectively compete for nutrients. According to Rotherham (2004) in nutrient limited soils, biomass accumulation of Rhododendron seedlings increased by 184% with mycorrhizal roots.

7. CONCLUSION

A dilemma surrounding Rhododendron confers this genus unique characters among the plant kingdom. Great ornamental values (spectacular flowers, species-richness, ease of hybridization and broad geographical range) will continue to make this shrub highly celebrated around the world. Its highly invasive ecophysiology (e.g. shade- and cold-tolerance, great resource use efficiency, allelopathy) and life strategy (e.g. plastic physiological, morphological, and behavioral response to varying environments and shifting between generative and vegetative reproduction as primary source of colonization), and difficulty to control will also continue to make this shrub a notorious woody weed world-wide. The broad geographical range and noteworthy similarities in climate, topography, and ecology of Rhododendron species can provide an opportunity to understand this notorious shrub species. Information transfer on the ecology and effective and cost-efficient control of Rhododendron may significantly improve management practices not only for the current Rhododendron-invaded ecosystems but also for other parts of the world where this shrub is becoming an ecological threat.

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