Ecology and traits of plant species that compete with boreal and temperate forest conifers: An overview of available information and its use in forest management in Canada

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ABSTRACT

In boreal and temperate forests in Canada, at least 71 plant species, including trees, shrubs, herbs, grasses, and ferns, have the potential to significantly reduce the growth of conifer regeneration. A thorough understanding of the autecology of these plants—their response to their environment—can help resource managers to improve their approaches to vegetation management, thereby maximizing crop tree growth and survival. In this paper, we highlight key sources of information about the autecology of the major species that compete with forest conifers, including books and field guides, journal series, Web sites, and plant trait databases. We suggest ways that this information can be applied in resource management, recommend approaches for maintaining and updating this information, and underline the needs for developing a single, consolidated, comprehensive source of such information for use by resource managers and researchers. Information gaps are also briefly discussed.

Key words: plant traits, life history traits, forest management, vegetation management, boreal forests, temperate forests

RÉSUMÉ

Dans les forêts boréales et tempérées du Canada, au moins 71 espèces végétales, incluant des arbres, des arbustes, des herbacées, des graminées et des fougères, ont le potentiel de réduire significativement la croissance de la régénération de conifères. Une compréhension approfondie de leur autécologie—i.e. leurs réponses à l'environnement—peut aider les aménagistes et les sylviculteurs à améliorer leurs approches en contrôle de la végétation, et ainsi, à maximiser la croissance et la survie des espèces désirées. Dans cet article, nous identifions des sources d'information clés sur l'autécologie des principales espèces qui entrent en compétition avec les conifères, incluant des livres, des guides terrain, des séries d'articles, des sites Internet et des bases de données sur les traits fonctionnels des plantes. Nous suggérons des manières d'utiliser ces informations dans l'aménagement forestier, et recommandons des pistes pour en assurer la mise à jour. Nous soulignons également le besoin de développer une source unique, consolidée et exhaustive pour ces informations, qui pourra être utilisée par les aménagistes et les chercheurs. Finalement, nous discutons brièvement des besoins supplémentaires en informations.

Mots-clés : caractéristiques des plantes, traits fonctionnels, aménagement forestier, gestion de la végétation concurrente, forêts boréales, forêts tempérées

Introduction

In Canada, competitive vegetation establishes rapidly on newly disturbed sites, often at the expense of the short-term survival and growth of crop trees, and particularly conifers (Wagner *et al.* 2001). Resource managers' views about this competitive vegetation continue to evolve. When focused on managing forests primarily for timber production, they viewed controlling competitive vegetation as an essential silvicultural practice that ensures an environment favourable to the survival and growth of conifer plantations established in temperate and boreal forests (Walstad and Kuch 1987, Wagner 1994). However, as they entered an era of more holistic ecosystem management (Christensen *et al.* 1996, Chapin *et al.*

2002, Burton *et al.* 2003), understanding the roles of competing vegetation in ecosystem function and developing management strategies that effectively address the tradeoffs between the benefits and the costs of competing vegetation became even more essential for effective silviculture (Simard and Durall 2004; Nilsson and Wardle 2005; Gilliam 2007; S. Haeussler, UBC, personal communication, 2011). This required not only a shift in thinking, but also new approaches and a better understanding of species' autecology.

Autecology is the branch of ecology dealing with the study of the responses and adaptations of individual species or populations to their environment (Barbour *et al.* 1987). Most of the principal competitive species in boreal and temperate

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forests are perennial plants that are highly adapted for rapid establishment and growth following a disturbance. Collectively, the set of characteristics (such as reproductive strategies that ensure regrowth or physiological adaptations to sunlight, heat, shade, and drought) that enable plants to respond to changes in their environment, are referred to as species' autecological traits. Understanding these traits may enable forest managers to develop more effective vegetation management strategies to maximize crop tree survival and growth. However, information about the autecological traits of Canadian boreal and temperate forest plant species is scattered in a plethora of journal publications, unpublished file reports, and online sources. With the introduction of sustainable forest management certification systems, which require clear documentation and increased accountability, consolidating the reliable information and making it more readily retrievable has become even more critical.

In this paper, we provide resource managers with (i) a list of key species that have potential to negatively affect the growth of boreal and temperate forest conifers, (ii) suggestions about how to apply plant ecology information (iii), an introduction to the primary sources of information (iv), an overview of available information, and (v) insight to future developments in this topical area. We believe that this information will assist resource managers to achieve their vegetation management, as well as other forest management objectives, which may range, for example, from promoting species that enhance wildlife habitat to controlling erosion, reducing insect or disease problems, and increasing opportunities for non-timber forest products.

Which Plants Have Potential to Negatively Affect the Growth of Boreal and Temperate Forest Conifers?

The term *competition* has been defined in many ways (Connell 1980, Booth *et al.* 2003, Radosevich *et al.* 2007), depending on the context in which it is used and the degree of emphasis on the mechanism or outcome of the interaction. In our current context, a definition given by Begon *et al.* (1996) is appropriate: competition is "an interaction between individuals, brought about by a shared requirement for a resource in limited supply, leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned." In addition to competing for resources, several species interfere with the survival and growth of coniferous crop trees by acting as secondary hosts for rusts and other pests (e.g., see Mihail *et al.* 2002), by causing physical damage, or via allelopathy (Rice 1984). "Compet-

ing species" may also improve conifer growth and survival by enhancing the recycling or fixing of nitrogen, ameliorating soil or air temperatures, and/or creating conditions less favourable to pests such as white pine weevil (Table 1). Competitive interactions comprise a complex balance of positive and negative exchanges among individuals (Brooker *et al.* 2008). These can be direct or indirect and more than one process may occur simultaneously between competing individuals, for example, both competition for light (negative effect) and increased nutrient cycling (positive effect) may occur. Thorough discussions about these interactions and their effects are available (see Booth *et al.* 2003, Radosevich *et al.* 2007, Brooker *et al.* 2008).

A list of species known or presumed to negatively affect the growth of boreal and temperate conifers and a brief summary of their key traits are provided in Table 2. This overview illustrates that an array of plants of varying growth forms can be considered significant competitors for conifers. Of these 71 species, 44 are shrubs, 10 are forbs, 8 are trees, 4 are grasses, 4 are ferns, and 1 is a sedge. From this list it is also evident that competition for light (43 species) is deemed more important or common than competition for moisture (34 species) and nutrients (27 species). In absolute terms, shrub species are the most abundant in each of the categories. All of the trees as well as some of the shrub (27), forb (4), fern (3), and grass (1) species can attain sufficient height and cover to significantly compete for light with boreal conifers. In relative terms, competition for soil water is mostly associated with grass species (three of four species), but some trees, shrubs, and herbaceous species also affect this resource. Most trees are also considered significant competitors for soil nutrients, and several shrub and herbaceous species (see Table 2 for references).

How Can Resource Managers Apply Plant Autecology Information?

Whether one is developing silvicultural strategies or attempting to understand the effects of silviculture on plant communities, familiarity with the autecological characteristics of plant species is essential (Wagner and Zasada 1991). Table 3 presents several questions related to the autecology of competitor species that resource managers may wish to consider before implementing silvicultural treatments.

Each plant species will respond differently to disturbances, such as mechanical, thermal, cultural, and chemical treatments (see Wiensczyk *et al.* 2011, this issue), due to differences in their life history characteristics, regeneration strategies, and physiology. The ability of a plant species to evade,

Table 1. Effects of non-crop vegetation on crop trees (adapted from Booth *et al.* 2003, Radosevich *et al.* 2007)

Negative	Positive
<ul style="list-style-type: none"> • Compete for site resources (e.g., light, moisture, nutrients, growing space) • Cause allelopathic interactions • Create sod/litter (restricts seed germination and seedling development, and inhibits soil warming) • Cause physical damage (e.g., snow press, smothering, whipping) • Provide habitat for damaging insects and small mammals • Act as alternate host for diseases 	<ul style="list-style-type: none"> • Moderate air and soil temperature extremes, reduce the vapour pressure deficit • Protect from insects (e.g., white pine weevil) • Capture, store and share nutrients, nitrogen fixation • Reduce physical damage from wind • Add organic matter to surface soils that may provide medium for soil microbes and may improve nutrient availability

Table 2. Competitive plants of the boreal and sub-boreal forest regions in Canada – their reproductive strategies, uses and benefits, and effects on conifers

Nomenclature		Sexual reproduction strategy ^b		Dispersal ^b					Vegetative reproductive strategy ^b					Competition for resources ^b		Resource enhancement ^b			Interference ^b				
Family	Species name ^a	seed	seed/spore bank	spores	wind	water	animals	gravity	sprouts	suckers	layers	stolons	rhizomes	light	moisture	nutrients	nitrogen fixing	mycorrhizae	nutrient cycling	allelopathy	physical	disease	environment
Tree	Betulaceae	x	–	–	x	–	–	–	x	–	–	–	–	x	–	x	–	–	–	–	–	–	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	–	x	–	x	–	–	x	–	–
	Pinaceae	x	–	–	–	–	x	x	–	–	x	–	–	x	x	x	–	–	–	–	–	x	–
	Salicaceae	x	–	–	x	x	–	–	–	x	x	–	–	x	x	x	–	–	–	–	x	–	–
	Salicaceae	x	–	–	x	x	x	–	–	x	x	–	–	x	x	x	x	–	–	–	–	–	–
Salicaceae	x	–	–	x	x	–	–	–	x	x	–	–	–	x	–	–	–	–	x	x	–	–	
Sapindaceae	<i>Acer rubrum</i> L.	x	–	x	x	–	–	–	x	x	*	–	–	x	–	x	–	–	–	–	x	–	–
Sapindaceae	<i>Acer saccharum</i> Marsh.	x	–	x	x	*	–	–	x	–	*	–	–	x	x	x	–	–	–	x	–	–	–
Shrubs	Adoxaceae	x	x	–	–	–	x	–	x	x	x	–	x	x	–	–	–	–	–	–	*	–	–
	Adoxaceae	x	x	–	–	–	x	–	x	x	x	–	x	x	x	–	–	–	–	–	–	–	–
	Araliaceae	x	–	–	–	–	x	–	*	–	*	–	*	x	x	–	–	–	–	–	–	–	–
	Betulaceae	x	–	–	x	–	–	–	x	x	x	–	–	x	x	x	x	–	–	–	–	–	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	x	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	x	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–
	Betulaceae	x	–	–	x	x	–	–	x	–	x	–	–	x	x	–	x	–	–	x	–	x	–

Table 2. (continued)

Growth form	Nomenclature		Sexual reproduction strategy ^b			Dispersal ^b				Vegetative reproductive strategy ^b							Competition for resources ^b			Resource enhancement ^b		Interference ^b				
	Family	Species name ^a	Common name	seed	seed/spore bank	seedling bank	spores	wind	water	animals	gravity	sprouts	suckers	layers	stolons	rhizomes	light	moisture	nutrients	nitrogen fixing	mycorrhizae	nutrient cycling	allelopathy	physical	disease	environment
Ericaceae	Ericaceae	<i>Chamaedaphne calyculata</i> (L.) Moench	leatherleaf	x	-	-	-	x	x	-	-	-	-	-	-	x	x	-	-	-	-	-	*	-	-	-
	Ericaceae	<i>Kalmia angustifolia</i> L.	sheep laurel	x	-	-	-	x	-	-	-	x	-	x	-	x	-	x	x	x	-	-	*	-	-	-
	Ericaceae	<i>Kalmia polifolia</i> Wangenh.	pale bog laurel	x	-	-	-	x	-	-	-	-	-	-	-	x	-	-	-	-	-	-	*	-	-	-
	Ericaceae	<i>Rhododendron groenlandicum</i> Oeder	common Labrador tea	x	-	-	-	x	x	-	-	x	x	x	-	x	-	-	-	x	-	-	*	-	x	-
	Ericaceae	<i>Rhododendron albiflorum</i> Hook.	white-flowered rhododendron	x	-	-	-	x	-	-	-	x	-	x	-	x	-	x	x	-	-	-	x	-	-	x
	Ericaceae	<i>Vaccinium angustifolium</i> Ait.	early lowbush blueberry	x	-	-	-	-	-	x	-	x	-	x	-	x	-	x	x	x	-	-	-	-	-	-
	Ericaceae	<i>Vaccinium membranaceum</i> Douglas ex Torr.	mountain huckleberry	x	-	-	-	-	-	x	-	x	-	-	-	-	x	x	x	x	-	-	-	-	-	-
	Ericaceae	<i>Vaccinium myrtilloides</i>	velvet-leaved blueberry	x	-	-	-	-	-	-	x	-	-	-	-	-	x	-	x	x	-	-	-	*	-	-
	Ericaceae	<i>Vaccinium ovalifolium</i> Sm.	oval-leaved blueberry	x	-	*	-	-	-	-	x	-	-	-	*	-	x	x	-	-	-	-	-	-	-	-
	Grossulariaceae	<i>Ribes glandulosum</i> Grauer	skunk currant	x	x	-	-	-	-	-	x	x	-	-	x	-	-	-	-	-	-	-	-	-	x	-
Grossulariaceae	Grossulariaceae	<i>Ribes hudsonianum</i> Richardson	northern black currant	x	*	-	-	-	-	x	-	-	-	*	-	-	-	*	-	-	-	-	-	-	x	-
	Grossulariaceae	<i>Ribes lacustre</i> (Pers.) Poir.	bristly black currant	x	*	-	-	-	-	x	-	-	-	*	-	-	-	*	-	-	-	-	-	-	x	-
	Grossulariaceae	<i>Ribes oxycanthoides</i> L.	Canada gooseberry	x	*	-	-	-	-	x	-	-	-	*	-	-	-	-	-	-	-	-	-	-	x	-
	Myricaceae	<i>Comptonia peregrina</i> (L.) J.M. Coult.	sweet-fern	x	x	-	-	-	-	-	x	-	-	-	-	-	x	-	x	-	-	-	-	*	-	x
Rosaceae	Rosaceae	<i>Amelanchier</i> spp.	serviceberry species	x	-	-	-	-	-	x	-	x	x	-	-	x	-	-	x	x	-	-	-	-	-	-
Rosaceae	Rosaceae	<i>Amelanchier alnifolia</i> (Nutt.) Nutt. ex M. Roem.	saskatoon	x	-	-	-	-	-	x	-	x	x	*	x	-	-	x	x	x	-	-	-	-	-	-
	Rosaceae	<i>Prunus pensylvanica</i> L. f.	pin cherry	x	x	-	-	-	-	x	-	x	x	-	-	-	-	x	x	x	-	-	-	-	-	x
	Rosaceae	<i>Prunus virginiana</i> L.	chokecherry	x	x	-	-	-	-	x	-	x	x	-	-	-	-	x	x	x	-	-	-	-	-	-
	Rosaceae	<i>Rosa acicularis</i> Lindl.	prickly rose	x	x	-	-	-	-	x	-	x	-	-	-	x	x	x	x	x	-	-	-	x	-	-
	Rosaceae	<i>Rubus allegheniensis</i> Porter	Allegheney blackberry	x	-	-	-	-	-	x	-	-	-	-	-	x	x	*	*	-	-	-	-	-	-	-
	Rosaceae	<i>Rubus canadensis</i> L.	Canada blackberry	x	-	-	-	-	-	x	-	x	-	x	-	x	x	*	*	-	-	-	-	-	-	-
	Rosaceae	<i>Rubus idaeus</i> L.	wild red raspberry	x	x	-	-	-	-	x	-	x	x	x	x	-	-	x	x	x	-	-	-	x	-	-
	Rosaceae	<i>Rubus parviflorus</i> Nutt.	sparse-flowered thimbleberry	x	x	-	-	-	-	-	x	-	x	-	x	-	-	x	x	-	-	-	-	*	-	-
	Salicaceae	<i>Salix</i> spp.	willow species	x	-	-	-	-	x	x	-	-	x	x	x	-	-	x	x	x	-	-	-	-	x	-
Sapindaceae	<i>Acer glabrum</i> Torr.	Rocky Mountain maple	x	-	-	-	x	-	-	-	-	x	-	-	-	-	x	x	x	-	-	x	-	-	-	
Sapindaceae	<i>Acer pensylvanicum</i> L.	striped maple	x	-	x	-	x	-	-	-	-	x	-	x	-	-	*	*	*	-	-	-	-	-	-	
Sapindaceae	<i>Acer spicatum</i> Lamb.	mountain maple	x	-	-	-	-	x	-	-	-	x	-	x	-	-	x	x	-	-	-	-	-	x	-	
Spiraeoideae	<i>Spiraea douglasii</i> var. <i>menziesii</i> (Hook.) C. Presl	Menzies' meadowsweet	x	-	-	-	-	x	-	x	-	x	-	-	-	x	x	-	-	-	-	-	-	-	-	-

Table 2. (continued)

Growth form	Nomenclature		Sexual reproduction strategy ^b		Dispersal ^b				Vegetative reproductive strategy ^b					Competition for resources ^b			Resource enhancement ^b			Interference ^b					
	Family	Species name ^a	Common name	seed	seed/spore bank	spores	wind	water	animals	gravity	sprouts	suckers	layers	stolons	rhizomes	light	moisture	nutrients	nitrogen fixing	mycorrhizae	nutrient cycling	allelopathy	physical	disease	environment
Herbaceous – forbs	Apiaceae	<i>Heracleum maximum</i> W. Barrtram		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Asteraceae	<i>Cirsium arvense</i> (L.) Scopoli	common cow parsnip	x	–	–	x	–	–	–	*	–	–	–	–	–	x	–	–	–	–	–	x	–	–
	Asteraceae	<i>Eurybia macrophylla</i> (L.) Cassini	Canada thistle	x	x	–	–	–	–	x	–	x	–	–	–	–	–	–	–	–	–	–	*	x	–
	Asteraceae	<i>Eurybia macrophylla</i> (L.) Cassini	large-leaved aster	x	–	–	–	–	–	–	–	–	–	–	–	x	–	x	–	–	–	–	*	x	–
	Convolvulaceae	<i>Convolvulus arvensis</i> L.	field bindweed	x	x	–	–	–	x	–	–	–	–	–	x	x	x	–	–	–	–	–	x	–	–
	Cornaceae	<i>Cornus canadensis</i> L.	bunchberry	x	–	–	–	–	x	–	–	–	–	–	–	x	–	*	–	x	–	–	–	–	–
	Fabaceae	<i>Lathyrus</i> spp.	peavine species	x	–	–	–	–	–	x	–	*	–	–	–	–	–	–	–	x	–	–	–	–	–
	Onagraceae	<i>Chamerion angustifolium</i> (L.) Holub	fireweed	x	–	–	x	–	x	–	–	–	–	–	–	x	x	x	–	–	–	x	x	x	x
	Rubiaceae	<i>Galium triflorum</i> Michx.	three-flowered bedstraw	x	–	–	–	–	x	–	–	–	–	–	–	x	–	–	–	–	–	–	x	–	–
	Urticaceae	<i>Urtica dioica</i> L.	stinging nettle	x	x	–	–	–	–	–	–	–	–	–	x	x	*	–	–	–	–	–	–	–	–
Valerianaceae	<i>Valeriana sitchensis</i> Bong.	Sitka valerian	x	–	–	–	x	–	–	–	–	–	–	–	x	x	x	x	–	–	–	x	x	–	
Herbaceous – grasses	Poaceae	<i>Calamagrostis canadensis</i> (Michx.) P. Beauv.	bluejoint reedgrass	x	–	–	x	–	–	–	–	–	–	–	x	x	x	x	–	–	–	–	x	–	x
	Poaceae	<i>Calamagrostis purpurascens</i> R.Br.	purple reedgrass	x	–	–	x	–	–	–	–	–	–	–	x	–	x	x	–	–	–	–	x	–	x
	Poaceae	<i>Calamagrostis rubescens</i> Buckley	pine reedgrass	x	–	–	x	–	–	–	–	–	–	–	x	x	x	x	–	–	–	x	x	–	–
	Pooideae	<i>Cinna latifolia</i> (Trevis. ex Goepp.) Griseb.	drooping woodreed	x	–	–	x	–	–	–	–	–	–	–	x	x	–	–	–	–	–	–	x	–	–
Herbaceous – sedge	Cyperaceae	<i>Carex concinnoides</i> Mack.	northwestern sedge	x	–	–	x	–	–	–	–	–	–	–	x	–	x	x	–	–	–	x	x	–	–
Herbaceous – ferns	Dryopteridaceae	<i>Dryopteris expansa</i> (C. Presl) Fraser-Jenkins & Jermy	spreading wood fern	–	–	x	–	–	–	x	–	–	–	–	x	–	–	–	–	–	–	–	x	–	–
	Hypolepidaceae	<i>Pteridium aquilinum</i> (L.) Kuhn	bracken fern	–	x	x	x	x	x	x	–	–	–	–	x	x	x	x	x	–	–	–	x	x	x
	Onocleaceae	<i>Matteucia struthiopteris</i> (L.) Todaro	ostrich fern	–	–	x	x	–	–	–	–	–	–	–	x	x	x	–	–	–	–	–	–	–	–
	Woodsiaceae	<i>Athyrium filix-femina</i> (L.) Roth	common lady fern	–	–	x	x	x	x	x	–	–	–	–	x	x	x	–	–	–	–	–	x	–	–

^aSpecies nomenclature follows VASCAN, the Database of Vascular Plants of Canada (Brouillet *et al.* 2010)

^bCoding: x = yes, * = possible, some evidence

Sources: Anderson (2001), Arnpur *et al.* (1995), Bell (1991), Bentley and Pinto (1994), Buse and Bell (1992), Campbell *et al.* (2003), Coladonato (1994), Gibson (1961), Haeussler *et al.* (1990), Harris (1990), Howard (1993), Louter *et al.* (1993), Mallik (1993), Matthews (1992), Ramovs and Roberts (2005), Steinberg (2001), Thiffault *et al.* (2004), Tirmenstein (1999), Tollefson (2007), Trindle and Flessner (2003), Uchytel (1989), Walkup (1991), Zouhar (2001)

Table 3. Examples of how autecological information can be used to support vegetation management treatment choices based on the types of questions resource managers might ask as part of their decision making process (adapted from Bell *et al.* 1998)

Vegetation management practices ^a	Type of Autecology Information				
	Plant species habitat requirements (e.g., light, water, nutrients)	Reproduction (i.e., vegetative and sexual)	Growth habit (e.g., longevity, form, growth rate)	Phenology (i.e., season timing)	Interaction with other trophic levels (e.g., wildlife habitat)
Silvicultural system	Will the system chosen provide optimum growing conditions for probable competitive species?	How will the existing species respond to clearcutting versus selection cutting?	How rapidly will the existing species reoccupy the site?	N/A	Which silvicultural system will maintain or enhance the habitat of early versus late seral wildlife species?
Physical (e.g., logging, thinning, mechanical site preparation)	Will there be a shift in site productivity due to water table changes or nutrient loss? Will rutting and compaction from heavy equipment favour additional species?	Will harvest and mechanical site preparation treatments control root suckering, bud banks, or persistent seed banks?	How rapidly will competitive species reoccupy the site?	Will the timing of harvest, site preparation, or manual cutting affect the regeneration of species such as aspen?	Will variable retention within clearcuts help to achieve habitat objectives? Will combining harvest and mechanical site preparation leave sufficient coarse woody material?
Thermal (e.g., prescribed burning)	Will site productivity be affected by organic matter and nutrient loss?	Will the intensity of fire control the persistent soil seed bank of species such as red raspberry?	How rapidly will competitive species reoccupy the site? Will species that root solely in the organic matter be extirpated from the site?	When is the most effective time to apply a prescribed burn?	What intensity of fire is required to achieve silvicultural objectives yet retain desired habitat?
Cultural (regeneration, livestock grazing, mulching)	Will choice, stocking, and density of tree species consume all available resources?	Will livestock grazing reduce the reproductive potential of the competitive plants?	Will livestock grazing introduce invasive species?	When is the most effective time during the season to apply livestock grazing given existing plant community?	What combination of tree species and canopy gaps will retain habitat?
Chemical (e.g., herbicides and fertilizers)	Will treatments increase available nutrients? Will resources such as light be reallocated to more competitive understory species such as Canada bluejoint grass?	What herbicide, rate, and application technique combination is required to control competitive species yet retain biodiversity?	Will overstory species composition be directly affected by the treatment?	When is the most effective time to apply herbicide treatments to control specific competitive species without harming crop trees? Will spring ephemerals be affected?	What combination of herbicide rates and application techniques are required to retain critical habitat?

^aSee Wienszyk *et al.* (2011) for information about the efficacy of forest management practices.

escape, or resist human-caused disturbance will ultimately depend on the traits it has developed to respond to various natural disturbances such as fire, browsing, insects, and disease (Bell *et al.* 1998).

Additional considerations for resource managers include the temporal nature of competition—its likeliness to persist—and the ability of individual species to pre-empt resources. These are captured in the dominance potential concept proposed by Newton (1973): “Dominance potential (DP) ... is the summation of all features of a species relating to its ability to assume dominance over a specific length of time in a limited system.” For a given site, a species with initial high dominance potential will tend to replace or suppress a species with lower DP unless action is taken to suppress the species with high DP or the species with lower DP is established first. A species with high “long-term” DP (e.g., trees) may prevail and eventually displace a species with high “short-term” DP (e.g., brush competitors).

What Are The Primary Sources of Plant Autecology Information?

Information about the autecology of plants is available in books, field guides, and journal series, as well as on Web sites and in plant trait databases, each of which are described in more detail below. In addition to this published and/or documented information, resource managers can apply local knowledge about species autecology. The literature is far from complete and may be inaccurate for local areas. Thus, local expert knowledge may be useful to supplement documented information.

Books and field guides

The first autecology guide was published in Germany (Kirchner *et al.* 1908–1936, cited in Klimešová and Klimeš 2008). This ambitious series remains incomplete but includes more than 300 species, which is more than what is included in most subsequent series. More recently, the characteristics of about 200 forest tree species and varieties are described in *Silvics of North America* (Burns and Honkala 1990). Most of the species included in this volume are native to North America, but a few are introduced and naturalized. Information on habitat, life history, and genetics is given for 15 genera, 63 species, and 20 varieties of conifers, and for 58 genera, 128 species, and 6 varieties of hardwoods. These include all of the trees presently considered commercially important in Canada.

The Woody Plant Seed Manual is a comprehensive handbook on the seeds of trees and shrubs of North America. Earlier versions include *Woody-Plant Seed Manual* (USDA 1948) with 420 taxa in 140 genera, and *Seeds of Woody Plants in the United States* (Schopmeyer 1974) with approximately 800 taxa in 188 genera. The current version contains almost 1,300 taxa in 230 genera (Bonner and Karrfalt 2008).

Since 1986, books and field guides that focus on plants that compete with boreal and temperate forest conifers have been published to assist resource managers in designing vegetation management strategies in British Columbia (Haeussler and Coates 1986, Coates *et al.* 1990, Haeussler *et al.* 1990), Ontario (Sims *et al.* 1990, Bell 1991, Buse and Bell 1992, Louter *et al.* 1993, Bentley and Pinto 1994, Arnup *et al.* 1995), and Quebec (Jobidon 1995). In total, these publications

describe 153 species: 8 conifer, 85 deciduous tree and shrub, 27 herb, 17 graminoid, 3 fern, 3 lichen, 3 moss, and 7 sphagnum species.

Journal series

In Great Britain, the *Biological Flora of the British Isles* series was started in 1941 and by the end of 1997 included more than 250 species. The most extensive biological floras following the British concept are published for the Moscow Region (Rabotnov 1974, cited in Klimešová and Klimeš 2008) and for the weeds of Canada—*The Biology of Canadian Weeds* (Cavers and Mulligan 1972); the latter includes about 144 species. A biological flora of Central Europe also contains relevant information (Poschlod *et al.* 1996). These journal series contain a wealth of botanical and scientific detail that is missing from the more practically oriented field guides described above.

Web sites

The internet is rich with information but much time and patience is required to ferret out what is reliable and relevant. Several useful and reliable online databases (Table 4) provide information about:

- Phylogeny, nomenclature, and/or rarity status – Canadensys and VASCAN, Flora of North America (FNA), FLORA Ontario – Integrated Botanical Information System (FOIBIS), and Northern Ontario Plant Database (NOPD)
- Species ecology – Fire Effects Information System (FEIS), USDA Plant Guides, and North European and Baltic Network on Invasive Alien Species (NOBANIS)
- Species distributions – plant hardiness

Plant Trait Databases

A trait is a plant characteristic, such as seed size, which can be measured at the scale of an individual species and has an effect on the species’ fitness and/or adaptation to an environmental constraint (Violle *et al.* 2007). Classifying species by shared biological characteristics, rather than their phylogeny, is increasingly recognized as a tool that is useful to identify common functional response groups among taxa (Grime 1988, Lavorel *et al.* 1997, Díaz and Cabido 2001). This approach is useful to resource managers because groups of plants with similar traits are likely to respond similarly to, for example, disturbance, and thus effective strategies can be developed for these groups rather than for each species individually. However, a thorough knowledge of species autecology is absolutely necessary to further develop this approach.

Since 1998, expansion of the development and use of plant trait databases (Table 5) has been rapid. Trait databases are increasingly used by the scientific community to model ecosystem responses to a variety of human-induced changes (e.g., see recent papers in the journals *Ecology*, *Nature*, and *Science*). They may also be useful in applied science (e.g., Aubin *et al.* 2008), as well as for assessing risk and developing silviculture guides (e.g., Bell *et al.* 1998).

Most of the existing databases are populated with information about European plant species (as per Table 5). This information is of some value to Canadian resource managers since some European species are invasive in Canadian forests. As well, databases are now being populated with what is known about Canadian species. These include TOPIQ (Aubin *et al.*

Table 4. Online databases that provide information about the phylogeny, nomenclature, rarity status and/or distribution of competitive species

Web site	Description	Source
Canadensys	<i>Canadensys</i> was created and maintained by The Montreal Biodiversity Centre. <i>Canadensys</i> was designed to share specimen information held by Canadian university-based biological collections and link this information via a network of distributed databases, compatible with other biodiversity information networks such as the Canadian Biodiversity Information Facility (CBIF) and the Global Biodiversity Information Facility (GBIF). Initially the network will focus on data from three of the most diverse and ecologically and economically important groups of organisms including plants.	http://www.canadensys.net/ [Accessed Jan. 12, 2010] http://data.canadensys.net/vascan/search/ [Accessed Jan. 12, 2010]
VASCAN	The <i>Database of Canadian Vascular Plants</i> (VASCAN) hosted by the <i>Canadensys</i> Web site provide an up-to-date, documented source of the names of vascular plants in Canada	http://data.canadensys.net/vascan/ [Accessed Dec. 7, 2011]
FEIS	<i>Fire Effects Information System</i> (FEIS) database was developed by the United States Department of Agriculture. FEIS contains literature reviews about the effects of fire for about 900 plant species, many of which compete with boreal and temperate forest conifers. Background information on taxonomy, distribution, basic biology, and ecology of each species are included.	http://www.fs.fed.us/database/feis/index [Accessed Oct. 9, 2010]
FOIBIS	<i>FLORA Ontario – Integrated Botanical Information System</i> (FOIBIS) was developed by the University of Guelph. FOIBIS provides information about phytogeography, rarity, and nomenclature for over 5000 plant species, including vascular plants, bryophytes and lichens that grow in Ontario. It includes native species as well as some ornamentals, weeds, invasive aliens, arctic disjuncts, and agricultural plants.	Newmaster and Subramanyam (2005) http://www.uoguelph.ca/foibis/ [Accessed Oct. 27, 2010]
Forestis	<i>Forestis</i> is a virtual herbarium hosted at Université Laval. The site is based on a powerful search engine that gathers hundreds of documents on any given species, each time it is used. The sources notably include digitalized herbarium and fresh plant specimens and scans from major North American and foreign flora collections.	http://forestis.rsvs.ulaval.ca/ [Accessed Nov. 4, 2010]
FNA	<i>Flora of North America</i> (FNA) presents information on the names, taxonomic relationships, continent-wide distributions, and morphological characteristics of all native and naturalized plants that occur in North America north of Mexico.	http://forestis.rsvs.ulaval.ca/ [Accessed Nov. 4, 2010]
NOBANIS	<i>North European and Baltic Network on Invasive Alien Species</i> (NOBANIS) is a gateway to information on alien and invasive species in North and Central Europe. NOBANIS provides fact sheets on many of the most invasive alien species in the region and include several species introduced from North America. These fact sheets include species distributions and recommended preventive, eradication, and control measures.	http://www.nobanis.org/default.asp [Accessed Oct. 28, 2010]
NOPD	<i>Northern Ontario Plant Database</i> (NOPD) was developed by Algoma University. NOPD provides access to over 55 000 herbarium specimens in northern Ontario educational and government institutions. NOPD also provides descriptions of many northern Ontario plant species to assist foresters, students, and interested members of the public in identifying local flora.	http://www.northernontarioflora.ca/ [Accessed Oct. 28, 2010]
Plant hardiness	<i>Plant hardiness</i> was developed by the Canadian Forest Service. It presents range maps for individual species of trees, shrubs, and perennial flowers that are based on climatic profiles for each plant using continent-wide climate models, supplemented by actual observations of plant occurrences	McKenney <i>et al.</i> (2001) http://planthardiness.gc.ca/ph_technicaldetails.pl?lang=en [Accessed Oct. 11, 2011]
USDA Plant Guide	<i>USDA Plants</i> provides facts sheets and plant guides for many species that occur in Canada. Fact sheets provide brief descriptions of a plant and its uses, and offer cultural recommendations, such as providing habitat for wildlife. Plant guides emphasize a particular aspect of a plant's biology and typically reference source documents. These products can be used with other tools available through PLANTS, especially VegSpec. VegSpec lets user select plants based on geography, a plant's adaptability to soils and climate, an intended conservation use, and other variables. After generating a shortlist using VegSpec, the fact sheets or plant guides are useful to learn more about each plant and its suitability for a specific purpose.	http://plants.usda.gov/ [Accessed Oct. 29, 2010]

Table 5. Functional plant trait databases available or in development worldwide

Name	Description	Source
BIOFLOR	Includes 66 traits for approximately 3660 vascular plants in Germany	Klotz <i>et al.</i> (2002) www.ufz.de/bioflor/index.jsp
BIOPOP	Provides ecological and life history traits of the vascular plants species of the Central European flora	Poschlod <i>et al.</i> (2000, 2003) http://www.floraweb.de/proxy/en/index.php
BROT	Summarizes fire-related traits for 859 vascular plant species of the Mediterranean Basin	Paula and Pausas (2008), Paula <i>et al.</i> (2009) http://www.uv.es/jgpausas/brot/BROT_2008.11.txt
CLO-PLA3	Outlines clonal growth and vegetative regeneration of vascular flora of Central Europe. CLO-PLA3 partly overlaps with the LEDA	Klimešová and Klimeš (2008) http://clopla.butbn.cas.cz/
EIBER	Indicates resprouting capacity (R) and the propagule persistence (P) of woody species growing in the eastern Iberian Peninsula (Mediterranean Basin)	Pausas <i>et al.</i> (2004), Pausas and Verdu (2005) Not available online
GLOPNET	Includes chemical, structural, and physiological traits of leaves for several species world-wide	Wright <i>et al.</i> (2004)
LEDA	Lists 46 life history traits for about 3,000 species of Northwest European flora; Focuses on 3 key features of plant dynamics: persistence, regeneration, and dispersal	Knevel <i>et al.</i> (2003), Kleyer <i>et al.</i> (2008) http://www.butbn.cas.cz/klimes/
SID (Seed Information Database)	Includes taxon-based information on a range of seed biological characteristics	Royal Botanic Gardens Kew (2008) Seed Information Database (SID). Version 7.1. (May 2008) http://data.kew.org/sid/
TOPIQ (Traits of Plants in Quebec)	Includes 650 vascular plant species of Quebec and Ontario; 41 traits are documented of which 23 are completed and validated	Aubin <i>et al.</i> (2007) Not available online
TRY	Is a global database of plant functional traits with >100 data contributors and >2 500 000 trait records compiled	http://www.try-db.org/index.php?n=Main.HomePage

2007) and TRY (Table 5). Unfortunately, access to information in the trait databases is currently largely restricted to members. Resource managers can obtain information either by working with a database member or becoming a member. Membership is typically gained by submitting a predetermined number of observations (e.g., 500) to encourage those who collect plant trait information to both contribute and benefit from the database.

What Information is Included in Autecology Guides and how is it Useful?

Autecology guides published in Canada (i.e., Haeussler and Coates 1986, Haeussler *et al.* 1990, Bell 1991, Louter *et al.* 1993, Bentley and Pinto 1994, Jobidon 1995) provide information about species' nomenclature, growth habit, reproduction, phenology, ecophysiology, and response to disturbance.

Nomenclature

Plants are given different common names and even scientific names evolve over time. For example, fireweed, also called great willowherb or rosebay willow herb, is known by various scientific names, including *Epilobium angustifolium*, *Chamaenerion angustifolium* and *Chamaenerion angustifolium*. This can make it difficult to find relevant information. The available autecology guides typically use regional nomenclature and, depending on when they were published, the scientific nomenclature used in these guides may no longer be preferred in published literature. An emerging approach is the use of DNA analysis to identify plant relationships, which is also influencing the evolution of naming conventions. If in doubt about a species name, resource managers can use online sources such as the *Integrated Taxonomic Information System* (ITIS; <http://www.itis.gov/info.html>), FOIBIS (<http://www.uoguelph.ca/foibis/>), or the *Database of Vascular Plants of Canada* (VASCAN) for confirmation (Table 4). VASCAN provides updated Canada-wide nomenclature and can be used as the standard reference (Brouillet *et al.* 2010; <http://data.canadensys.net/vscan/>).

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Description

Autecology guides typically provide brief written descriptions and illustrations of stems, leaves, flowers, and fruits for selected species. These are not intended as comprehensive taxonomic descriptions. Since the morphology of a species

may change across its distribution, we recommend that resource managers use local plant identification guides to identify plants with certainty.

Distribution

Distribution maps can be used as indicators of where competitive plants may occur. However, these maps are not always accurate due to, for example, to lack of knowledge and/or resolution of mapping. As well, existing models that predict plant migration may overestimate the speed at which plant distributions will change as the climate changes and detailed maps produced in the 20th century may be rapidly outdated. Since the autecology guides are relatively static, resource managers are encouraged to visit the national plant hardiness-related web site (<http://www.planthardiness.gc.ca/>), which is more likely to provide updated information about potential distributions based on climate suitability.

Habitat requirements

Habitat requirements include the site and soil types where a species is likely to be found, and information about how it consumes light, water, and nutrients. Regional forest ecosystem classification (FEC) information linked to plants species, e.g., Klinka *et al.* (1989) and Beaudry *et al.* (1999, 2003) provide information for British Columbia, and Sims *et al.* (1990), Bell (1991), and Bentley and Pinto (1994) provide that for Ontario. Combined with some knowledge of plant resource requirements, resource managers can use this information to develop site-specific silvicultural practices to promote or retard the growth of selected species. With the addition of climatic tolerances, such as temperatures and precipitation, the effects of climate change on species distributions can be modelled (McKenney *et al.* 2001). At present, resource use and climatic tolerance for many understory species are poorly understood and are topics that require future research.

Reproduction

Knowledge of reproductive strategies can be used to predict species responses to disturbance. Plant species with high reproductive capabilities are more difficult to control and easier to promote than species with limited reproductive capabilities.

Almost all competitive plants reproduce both vegetatively and sexually. Sexual reproduction includes the current seed crop for seed-producing species as well as the seed bank for species (e.g., pin cherry, red raspberry) with seed that remain viable in the soil for extended periods. Vegetative reproduction strategies include regeneration from roots (suckering) and rhizomes as well as regeneration from shoots (root collar or lower stem sprouts), stolons, layering (Table 2), or by fragmentation. Although not included in Table 2, fragmentation is an important method of regeneration for balsam poplar (*Populus balsamifera* L.), some willows, lichens, and various other plants. Most plant species have more than one strategy; thus, their response to treatment will depend on the type and severity of disturbance (Wiensczyk *et al.* 2011) as well as other factors such as timing during the year or the plant's life stage.

Following a low-intensity disturbance, vegetative reproduction is generally more important in the rapid recovery of plant cover than sexual reproduction (Roberts 2004). For example, sprouting from suckers connected to parent plants with established food reserves and water supply (Zasada 1971) facilitates regrowth of site-adapted individuals regard-

less of seed supply, dispersal, viability, or seedbed conditions.

Following a high-intensity disturbance, seed production (see Schopmeyer 1974, Young and Young 1992) will be important in the species colonization phase (Roberts 2004). Species that reach sexual maturity and produce large amounts of seed early in their life cycle have a competitive advantage over those that first produce seeds at older ages (Zasada 1988). Silvicultural disturbances can be timed according to knowledge of seed arrival, as many wind-borne seeds have limited viability and new seedlings cannot compete with established plants (Marks 1974).

Knowledge of seed longevity in the soil helps resource managers to understand and predict plant population dynamics and response to disturbances as well as to design effective vegetation management strategies (Wiensczyk *et al.* 2011). Following timber harvest, fire, or another major disturbance in a mature forest stand, infrequent species may become established from buried seeds and quickly dominate the pioneer vegetation community. Seeds buried in the organic layer and upper mineral soil (seed bank), some of which remain dormant in the soil for many years, germinate in response to increased light, soil temperature, or other changes following site disturbance (Conn and Farris 1987, Kramer and Johnson 1987). Seed bank species composition and seed densities will vary greatly from site to site (Kramer and Johnson 1987) and vegetation management strategies will need to be adjusted accordingly.

For comprehensive reviews of the sexual reproduction of plants, refer to *Seeds of Woody Plants in North America* (Young and Young 1992), *Seed Ecophysiology of Temperature and Boreal Zone Forest Trees* (Farmer 1997) and *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination* (Baskin and Baskin 2001).

Propagation

Plant propagation is the multiplication of plants by both sexual and asexual means (Dirr 1990). An understanding of propagation techniques can be used in research and rehabilitation projects. Several of the existing autecology guides include information about seeding, vegetative propagation, micropropagation, and transplanting.

Growth habit

The growth habit of a plant determines its relative competitiveness in a forest community, and includes life cycle (e.g., annual, biennial, or perennial), life form (herb, shrub, or tree), longevity, and growth pattern. Annuals and biennials complete their life cycles after producing seeds in one and two years, respectively. With such a short life span, annuals and biennials rarely constitute a serious obstacle to conifer regeneration. They may, however, reduce height growth of and occasionally even smother (through snow load) small conifer seedlings (Bell *et al.* 1998). Perennials (trees, shrubs, and herbs that live for more than two years) may create greater competition through rapid spring growth from overwintered roots and shoots or rapid recovery following a disturbance. For instance, perennial grasses form thick mats that impede seedling establishment by creating an unsuitable seedbed, shading, and contributing to winter smothering (Bell 1991). Another example is the tall broad-leaved shrub mountain maple (*Acer spicatum* Lamb.) that persists through all stages of succession and can create a dense canopy after disturbance,

drastically reducing the availability of light reaching the ground (Aubin *et al.* 2005). All species listed in Table 2 are perennials.

Growth patterns (e.g., stem height, clone size, rooting zone, and root grafting) also contribute to a plant's competitive status and influence how they respond to management treatments or disturbances. For example, the maximum height that a species can achieve will determine if it will be a competitor for only a few or many years. Root grafting enables subordinate plants to obtain nutrients from dominant plants and may also enable the transfer of herbicides from one individual to another.

Phenology

Phenology is the study of the timing of life-cycle events in relation to environmental cues. It includes the timing of growth events such as bud break, shoot elongation, bud set, flowering, seed set and fall, carbohydrate movement, leaf colouration and drop, frost hardening, and dormancy (Wagner and Zasada 1991). Timing of root development, for example, affects the uptake of moisture, nutrients, and soil-active herbicides (Bell *et al.* 1998).

Phenological information is essential to achieve maximum efficacy from vegetation management treatments, including prescribed fire (Noste *et al.* 1987), motor-manual cutting (Harrington 1984, Jobidon 1997, Bell *et al.* 1999) and herbicides (Bell *et al.* 2000, Bell and Pitt 2007). Most autecology guides provide information about shoot phenology (i.e., timing of leaf flush, radial expansion, and dormancy) and reproductive phenology (i.e., time of flowering, seed maturation and seed fall) that can be used, for example, to determine optimum treatment timing (see Bell and Pitt 2007).

Interactions with other trophic levels

Existing autecology guides provide some information about the relationship between animals and plants, with emphasis primarily on damaging effects (e.g., moose defoliation). In a study in Minnesota, Posner and Jordan (2002) concluded that browsing by moose reduced the height of shrubs competing with white spruce saplings, providing a release effect. Similarly, using exclosures to keep moose out of experimental plots on the island of Newfoundland, McLaren *et al.* (2009) reported that balsam fir outside the fenced plots where moose were free to browse on competing hardwoods were larger than those inside the enclosure where competition from hardwoods was not reduced.

Positive interactions between plants and animals (such as control of major pests) have received less attention. For example, in their comprehensive review of the relationships between spruce budworm and birds, Venier and Holmes (2010) concluded that birds influence budworm cycles at endemic population levels through predation of large larvae and pupae. Also, while bird predation is not the primary cause of budworm population variations, it may help to determine the mean level of oscillations (and by inference the amount of resultant damage)

What Lies Ahead?

During the 1990s, several regional autecology guides were prepared and distributed to resource managers in British Columbia, Ontario, and Quebec. These guides served their original purpose of providing resource managers with information

about "weed species", but they are rapidly becoming outdated. Up-to-date information is needed for more than just species that were once considered weeds. Demand is growing for information about rare and invasive species and species other than trees that have commercial value or important roles in ecosystem function, such as nutrient or carbon cycling. Knowledge about the effects on forest species of changes in climate is also required. As well, additional information on the complex interactions among crop trees, their competitors, and organisms from other trophic levels is needed to provide resource managers with a more comprehensive understanding of ecosystem dynamics and how these are influenced by silvicultural treatments (Puettmann *et al.* 2008).

Given these demands, now is the time to aggregate the existing guides into a single, standardized, and current source that can be accessed by both resource managers and the scientific community. As well, an urgent need exists to incorporate the information into a user-friendly national database, such as *Traits of Plants in Canada* (TOPIC), and international trait databases such as TRY (Table 4). Once this happens, resource managers across Canada can look forward to easily accessible and comprehensive information about plant autecology for use in future resource management decision-making.

Acknowledgements

We are grateful to the Agricultural Research Institute of Ontario (ARIO) for sponsoring ongoing work on the autecology of forest plants, to the many individuals who provide information about the autecology of forest plants through their books, journal papers, Web sites, and plant trait databases and to Lisa Buse, Sybille Haeussler, Kandyd Szuba, Denise Tousignant, and Bob White for reviewing and commenting on earlier versions of this manuscript.

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