RISING CARBON DIOXIDE AND INVASIVE, NOXIOUS PLANTS: POTENTIAL THREATS AND CONSEQUENCES

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ABSTRACT

Although carbon dioxide (CO_2) is the principle greenhouse gas, it also represents the sole source of carbon for plants, and hence for almost all terrestrial life. Because current levels of atmospheric CO_2 are less than optimal for plant growth, recent and projected increases in this gas are expected to stimulate the growth of a number of plant species. Although this aspect of climate change can be viewed as beneficial, the rise in carbon dioxide is indiscriminate in stimulating the growth of both wanted and unwanted plants. Because international trade has increased the biotic mixing of flora across many parts of the globe, unwanted plant species are becoming widely established. The severity of damage induced by these species and their panoptic scale have produced a new class of unwanted plants: invasive, noxious weeds. To determine whether rising carbon dioxide has been a factor in the establishment and success of such plants, we have compared the potential response to recent and projected changes in carbon dioxide between invasive, noxious species and other plant groups, and assessed whether CO_2 preferentially selects for such species within ecosystems. A synthesis of literature results indicates that invasive, noxious weeds on the whole have a larger than expected growth increase to both recent and projected increases in atmospheric CO_2 relative to other plant species. There is also evidence that rising CO_2 can, in fact, preferentially select for invasive, noxious species within plant communities. Furthermore, there is initial data suggesting that control of such weeds may be more difficult in the future. However, the small number of available experiments

make such conclusions problematic, and emphasize the urgent need for additional studies to address the biological and economic uncertainties associated with CO_2-induced changes in the ecology of invasive, noxious weeds.

INTRODUCTION

Weeds, strictly speaking, do not exist in nature; rather, weeds are recognized by humans as "plants out of place"; that is, plants whose presence is undesirable or objectionable. The degree of undesirability may be related to limiting the growth of a desired plant (e.g., velvetleaf in cotton), its impact on public health (e.g., ragweed), or a negative aesthetic value (crabgrass in a flower garden).

Weeds are defined therefore, by human activities, particularly land use management. For example, soil preparation in agriculture, clearing land for construction, cutting timber, etc. create regular disturbances that often provide opportunities for weed seed establishment. Many plants considered weeds, are, in fact, adapted to take advantage of these disturbed conditions through vigorous growth, prodigious seed production, and seed longevity (see Baker, 1974).

Because alteration of land use has been an intrinsic characteristic of all human societies, weeds have been a recognized affliction since civilization's beginnings. Currently in the U.S., where labor is expensive and herbicide use is widespread, production losses in agriculture due to weeds average about 7%, but if no herbicide is used, production losses average about 35% (Bunce and Ziska, 2000). In the United States, more than $6 billion is spent on weed control every year (Patterson and Flint, 1990). Globally, the impact of weeds on cropping systems rivals that of insects, diseases and unfavorable weather. In rice, for example, direct production losses are estimated at 20%, with losses climbing to 100% if weeds are not controlled (IRRI, 2002). Weeding is also a considerable economic cost in rice production systems, with estimates of 50-150 person days per hectare required for manual weeding. Because of the human cost associated with weed control in developing countries, a global economic estimate associated with weed control is difficult, but would certainly be an order of magnitude greater than that for the U.S. (IRRI, 2002).

INVASIVE, NOXIOUS WEEDS

Clearly, human activities related to land use carry a large economic cost associated with weed control. However, in addition to these established costs, there is mounting concern that new human activities will further exacerbate the economic and/or environmental risks associated with weed containment.

One such activity is related to the significant increase in global trade during the later part of the 20th and beginning of the 21st century. As noted by Mooney and Hobbs (2000), global trade has transformed biogeographically distinct flora and fauna into a massive biotic "soup," with species becoming intermingled across countries and cultures. This accidental mixing has lead to the introduction of a number of new weeds (and new insects and diseases as well) into locations hitherto unknown. For weedy species, the result has been a number of newly established, aggressive plants with such high population densities that widespread damage to crops, rangelands, forests and aquatic systems is unprecedented (Table 1). Because these species are non-endemic for a region, they are referred to as exotic, alien, introduced or invasive species. While "invasive" remains the most popular descriptive term, it should be emphasized that not all plant species transported between continents are damaging, many are, in fact, necessary for economic trade. An additional term, "noxious," has therefore been suggested to describe not only a nonnative, invasive species, but one that induces widespread economic or environmental damage (Table 1) (Skinner et al., 2000). Legally, a noxious weed is any plant designated by a Federal, State or county government as injurious to public health, agriculture, recreation, wildlife or property. Unfortunately, at present there is not always agreement among policymakers at the State or Federal level as to what even constitutes a noxious weed (e.g., kudzu, Table 1).

Nomenclature aside, the impact of this new weed threat is unprecedented. An estimated 2,000 alien plant species have become established in the continental United States. The U.S. Department of Agriculture estimates the annual productivity loss of 64 crop species due to noxious species at $7.4 billion (USDA-NRCS, 1999). This estimate does not consider economic damages (e.g., property damage) due to changes in fire-frequency induced by the spread of invasives such as cheatgrass (*Bromus tectorum*), a species that alters the fire cycle from 20-25 years to 3-5 years (Smith et al., 1987); it does not consider denigrations in rangeland productivity associated with the spread of such invasive, noxious weeds as Canada thistle (*Cirsium arvense*), spotted knapweed (*Centaurea maculosa*) or yellow star thistle (*Centaurea solstitialis*), nor does it consider changes in water rights, acquisition or quality associated with the spread of water hyacinth (*Eichhornia crassipes*). While precise economic damages are difficult to assess, it has been estimated that the spread of noxious weeds and their subsequent mitigation/control may exceed $30 billion each year (Pimental et al., 1999).

There is also a significant environmental cost of noxious weeds. E.O. Wilson, the noted ecologist has observed that, "On a global basis, the two great destroyers of biodiversity are, first habitat destruction and, second, invasion by exotic species." (1999). It has been estimated that more than 200 million acres of natural habitats (primarily in the Western U.S.) have already been lost to invasive, noxious weeds, with an ongoing loss of 3000 acres a day (Westbrooks, 1998). The plant species that are most harmful to native biodiversity are those that significantly change ecosystem processes, to the detriment of native species. Unfortunately, this applies to a number of invasives, but two that are particularly destructive are cheatgrass (*B. tectorum*), which increases fire frequency, eliminating native species that cannot survive frequent and widespread burns; and, salt cedar (*Tamarix ramosissima*), which uses ground water at such a prodigious rate that it limits the survival of other endemic tree species.

Table 1 Partial list of recognized noxious invasive weeds at the Federal and/or State level for four principal habitats. This is only a partial list, more than 600 weeds are now recognized as noxious invasives in North America (plants.usda.gov/index.html). Note that some weeds may appear in more than one habitat.

Habitat	Common Name	Scientific Name	Federal Noxious*	State Noxious†
Agriculture	Velvetleaf	*Albutilon theophrasti*		4
	Animated oat	*Avena sterilis*	Y	9
	Whitetop	*Cardaria draba*		15
	Musk thistle	*Carduus nutans*	Y	24
	Canada thistle	*Cirsium arvense*		31
	Bull thistle	*Cirsium vulgare*		9
	Field bindweed	*Convolvulus arvensis*		22
	Dodder	*Cuscuta* spp.	Y	8
	Nutgrass	*Cyperus* spp		4
	Morning-glory	*Ipomoea* spp.		2
	Brownbeard rice	*Oryza rufipogon*	Y	9
	Wild sugarcane	*Saccharum spontaneum*	Y	9
	Field sowthistle	*Sonchus arvensis*		13
	Johnson grass	*Sorghum halepense*		18
	Asiatic witchweed	*Striga asiatica*	Y, quarantined	11
Aquatic/ Wetland	Giant Reed	*Arondo donax*		1

	Feathered mosquitofern	*Azolla pinnata*	Y	7
	Caulerpa	*Caulerpa taxiflora*	Y	6
	Water hyacinth	*Eichhornia crassipes*		6
	Waterthyme	*Hydrilla verticillata*	Y	15
	Swamp morning-glory	*Ipomoea aquatica*	Y	9
	Asian marshweed	*Limnophila sessiliflora*	Y	8
	Purple loosestrife	*Lythrum salicaria*		30
	Black mimosa	*Mimosa pigra*	Y	10
	Parrot feather	*Myriophyllum aquaticum*		4
	Ducklettuce	*Ottelia alismoides*		7
	Kariba-weed	*Salvinia molesta*	Y	12
	Brazilian peppertree	*Schinus terebinthifolius*		2
	Common cordgrass	*Spartina anglica*		2
	Saltcedar	*Tamarix ramosissima*		9
Forest/ Woody	Black wattle	*Acacia mearnsii*		1
	Tree of heaven	*Ailanthus altissima*		1
	Garlic mustard	*Alliaria petiolata*		4
	Japanese honeysuckle	*Lonicera japonica*		1
	Melaluca	*Melaluca quinquenervia*	Y	8
	Malabar melastome	*Melastoma malabathricum*	Y	10
	Velvet tree	*Miconia calvescens*		1
	Black mimosa	*Mimosa pigra*	Y	10
	Mile-a-minute weed	*Polygonum perfoliatum*		5
	Japanese knotweed	*Polygonum cuspidatum*		5
	Syrian mesquite	*Prosopis farcta*	Y	9
	Kiawe	*Prosopis pallida*	Y	9

	Kudzu	*Pueraria Montana*		9
	Brazilian peppertree	*Schinus terebinthifolius*		2
	Tropical soda-apple	*Solanum viarum*	Y	12
Rangeland/ Pasture	Jointed goatgrass	*Aegilops cylindrical*		7
	Cheatgrass	*Bromus tectorum*	Y	11
	Spotted knapweed	*Centaurea maculosa*		15
	Yellow star-thistle	*Centaurea solstitialis*		12
	Bull thistle	*Cirsium vulgare*		9
	Poison hemlock	*Conium maculatum*		8
	Common crupina	*Crupina vulgaris*	Y	15
	Quackgrass	*Elytrigia repens*		5
	Leafy spurge	*Euphorbia esula*	Y	20
	Cogongrass	*Imperata cylindrical*	Y	9
	Dyer's woad	*Isatis tinctoria*		11
	Kikuyu grass	*Pennisetum clandestinum*	Y	9
	Itchgrass	*Rottboellia cochinchinensis*	Y	11
	Puncturevine	*Tribulus terrestris*		9

* Federally regulated weeds that are restricted by plant protection and/or quarantine.
† The number of states that have designated this species as a noxious weed.

RISING CARBON DIOXIDE AND PLANT GROWTH

Given their significance, it is imperative that we recognize those factors that contribute to the biological success and continued spread of invasive, noxious weeds. This is necessary to limit their impact, but also to design effective control measures. Overall, three main factors are thought to contribute to their success: lack of natural enemies (Settle and Wilson, 1990), the physical environment (Moyle and Light, 1996), and available resources (Sher and Hyatt, 1999; Petren and Case, 1996). Lack of natural predators and parasites for an introduced species and a physical environment that match the species previous condition are, of course, significant factors in determining whether an introduced species becomes noxious, and are considered in a number of relevant books and scientific articles relevant to the issue (e.g., Mooney and Hobbs, 2000; Ruiz and Carlton, 2003). But it is in the area of plant resources that human activity may be contributing to the potential success of noxious weeds. Plant resources can be divided into four essential categories: light, water, nutrients and carbon dioxide. Changes in any of these resources will alter plant growth and influence competition in plant communities.

One such resource, increasing at a rapid rate as a result of both deforestation and the burning of fossil fuels, is the amount of carbon dioxide in the atmosphere. Since the mid-1950s, records of carbon dioxide concentration ([CO_2]) obtained from the Mauna Loa observatory in Hawaii have shown an increase in [CO_2] of about 20% from 311 to 375 parts per million (ppm) (Keeling and Whorf, 2001). The current annual rate of [CO_2] increase (~0.5%) is expected to continue with concentrations exceeding 600 ppm by the end of the 21st century (Schimel et al., 1996). Interestingly, because the observatory at Mauna Loa and other global monitoring sites (cdiac.esd.ornal.gov/home.html) sample air at high elevations, away from anthropogenic sources, actual ground-level [CO_2] can be significantly higher. For example, urban areas in Phoenix and Baltimore show [CO_2] values exceeding 500 ppm, and suburban values near Washington, D.C. and Sydney, Australia, report [CO_2] above 420 ppm (Idso et al., 1998, 2001; Ziska et al., 2001). This suggests that while the Mauna Loa data may reflect [CO_2] for the globe as a whole, regional increases in [CO_2] may already be occurring as a result of urbanization.

Carbon from CO_2 fixed through photosynthesis constitutes about 45-50% of plant dry matter (Houghton et al., 1985). Because CO_2 remains the sole source of carbon for plant photosynthesis (and hence, 99% of all living terrestrial organisms), and because at present, [CO_2] is less than optimal for photosynthesis, as atmospheric [CO_2] increases, plant growth will be stimulated accordingly. In fact, increasing [CO_2] has been shown to significantly stimulate growth and development in hundreds of plant species (see Kimball, 1983; Kimball et al., 1993; Poorter, 1993 for reviews examining the response to future CO_2 concentrations; Sage, 1995 for a review of the response to pre-industrial CO_2 concentrations).

RISING CO_2 AND INVASIVE, NOXIOUS WEEDS: PLANT RESPONSE TO PROJECTED CHANGES

Given that plant photosynthesis and growth are stimulated by increasing [CO_2], is a strong response to increasing [CO_2] a common characteristic of invasive plant species? It has been speculated that the growth response of invasive, noxious species to increasing [CO_2] may be particularly strong (Moore, 2004). If so, then adaptation of invasive, noxious weeds to rising [CO_2]and the subsequent increase in growth and seed dispersal may be an overlooked factor in their establishment and success. At present more than 600 noxious and/or invasive plant species have been identified in North America alone (plants.usda.gov/index.html). Although a number of reviews have speculated on the response of noxious weeds to rising [CO_2] (Shea and Chesson, 2002; Weltzin et al., 2003; Dukes and Mooney, 1999), few studies have actually quantified the response of individual plants to future, projected increases in atmospheric carbon dioxide concentration (Huxman et al., 1999; Dukes, 2002; Ziska, 2003a).

Although invasive agronomic weeds are a growing threat to agronomic productivity (Table 1), only a handful of studies have examined their response to projected increases in atmospheric [CO_2]. Among these, Canada thistle (*Cirsium arvense*), shows the strongest growth response, increasing by 75% (Table 2). This is potentially worrisome given that Canada thistle is ranked as the number one invasive agronomic weed (Skinner et al., 2000). Of additional concern, is that no data are available for many of the invasive agronomic weeds that are wild relatives of those species brought into the U.S. as crops. These weeds (e.g., wild sugarcane, wild rice and animated oat) are considered among the most troublesome because they are genetically similar to the crop, and many of the farming practices (planting date, fertilizer requirement, etc.) benefit the growth and reproduction of both the domestic crop and its wild relative.

Although the impact of invasive, aquatic weeds (Table 1) is global in scope (e.g., water hyacinth is among the worst noxious weeds in Africa), to date, almost nothing is known regarding their response to rising carbon dioxide (e.g., a single study on waterthyme, Table 2). Admittedly, it is difficult to experimentally manipulate [CO_2] (as dissolved carbonate) in submersible vegetative plant parts, but this does not explain why no data on [CO_2] responsiveness exists for above ground leaves in aquatic systems or for riparian weeds such as salt cedar (*T. ramosissima*) or purple loosestrife (*Lythrum salicaria*).

A similar lack of information is evident for invasive, noxious woody species as well (Table 1), with two notable exceptions (Table 2). Sasek and Strain (1991) observed that after 54 days of exposure to 675 ppm CO_2, Japanese honeysuckle (*Lonicera japonica*) had three-fold the response as coral honeysuckle (*L. sempervirens*, a native vine) when compared to current levels of CO_2 (135% vs. 40%). They also observed that the total biomass of kudzu (*Pueraria montana*, var. *lobata*) doubled after 24 days of exposure to the same CO_2 range (Sasek and Strain, 1988). Sasek and Strain (1990), also noted that the current latitudinal distribution of kudzu was limited to south of the Ohio valley and the Mason-Dixon line by low winter temperatures (see Figure 7, Sasek and Strain, 1990). Interestingly, recent observations have noted kudzu populations near the Chicago area (www.chicagobotanic.org) and northwestern Massachusetts (www.cyberonic.com). How much of this distribution is due to increasing winter temperatures is unclear, but the northward spread is consistent with the Sasek and Strain predictions.

Table 2 Overview of potential response of selected noxious, invasive weeds to either recent or projected changes in the concentration of atmospheric carbon dioxide [CO_2]. Recent changes refer to the increase in [CO_2] from 250-300 ppm (sub-ambient) to 360-400 ppm (current ambient concentration); projected changes refer to the increase in [CO_2] from 360-400 ppm to 600-800 ppm, a value expected to occur before the end of the current century. Values given are the ratio of plant biomass produced at the two [CO_2] comparisons (i.e., a value of 1 indicates no response to increasing CO_2 while a value of 2 indicates a doubling in biomass). NA=not available.

Species	Common Name	Recent	Projected	Reference
Albutilon theophrasti	Velvetleaf	1.3-1.58	0.88-2.29	Bazzaz et al., 1989; Bunce, 2001; Dippery et al., 1995; Morose and Bazzaz, 1994.
Ambrosia artemisiifolia	Annual ragweed	NA	1.22-1.57	Bazzaz and Carlson, 1984; Hirose et al., 1996.
Aveno fatua	Wild oat	NA	1.84	Freeden and Field, 1995.
Brassica kaber	Wild mustard	NA	1.27-1.30	Wayne et al., 1999.
Bromus madritensis	Red brome	NA	1.09-1.51	Huxman et al., 1999; Smith et al., 2000.
Bromus tectorum	Cheatgrass	NA	1.39-1.93	Poorter, 1993; Smith et al., 1987.
Centaurea maculosa	Spotted knapweed	2.15	1.46	Ziska, 2003a.
Centaurea solstitialis	Yellow star-thistle	1.87	1.15-1.68	Dukes, 2002; Poorter et al. 1996; Ziska, 2003a.
Cirsium arvense	Canada thistle	1.58-2.84	1.69-1.70	
Convolvulus arvensis	Field bindweed	1.85	1.36	Ziska ,2003a.
Datura stromonium	Jimsonweed	NA	1.76	Garbutt and Bazzaz, 1984.
Elytrigia repens	Quackgrass	NA	1.12-1.68	Tremmel and Patterson, 1993; Ziska and Teasdale, 2000.
Euphorbia esula	Leafy spurge	1.95	1.43	Ziska, 2003a.
Hydrilla verticillata	Waterthyme	NA	1.04-1.46	Chen et al., 1994.
Lonicera japonica	Japanese honeysuckle	NA	2.34-3.60	Belote et al., 2003; Sasek and Strain, 1988.
Prosopis glandulosa	Honey mesquite	1.53	1.11-1.37	Polley et al., 1994; 1996; 2002.
Pueraria montana	Kudzu	NA	1.20-2.15	Sasek and Strain, 1991.
Sonchus arvensis		2.09	1.66	Ziska, 2003a.

Because of their recent impact on rangeland and forage production, invasive, noxious weeds have received considerably more attention than in other plant communities. The result has been that a number of acknowledged troublesome species (Table 1) have been evaluated with respect to projected CO_2 levels (Table 2). All invasive species tested show a positive growth and biomass response too increased [CO_2], although the range is variable depending on species (Table 2). It is worth noting that early successional species associated with altering fire frequency (e.g., *B. tectorum)* as well as woody vines (e.g., *L japonica*) can demonstrate a strong growth response to a projected doubling of [CO_2] (Table 2).

Relative to other plant species, do invasive weeds show a stronger or lesser response to increasing atmospheric [CO_2]? What is the expected response? One of the earliest attempts to integrate plant response to elevated [CO_2] was published by Kimball (1983) who examined 430 previous studies. Based on his analysis he determined that the average response of plants ($\pm$SE) to future elevated CO_2 conditions was 34 $\pm$6% (330-360 ppm CO_2 for ambient vs. 600-1000 ppm [CO_2] for future elevated, Kimball, 1983). Other studies that have quantified the variation in the response of plants to future [CO_2] show similar results (e.g., 37% for 156 plant species, Poorter, 1993). For the current literature assessment, while the response of some species fall within the expected range, a number of species show a doubling or tripling of size (Table 2). Overall, the average response to projected [CO_2] increases was approximately 60%, suggesting a significantly stronger than anticipated growth response for invasive, noxious species (Table 2).

RISING CO_2 AND NOXIOUS WEEDS: PLANT RESPONSE TO RECENT CHANGES

But atmospheric [CO_2] is in flux. It has already risen from ~285 to 378 ppm during the 20th century, with most of the observed increase coming since the late 1950s (circa 312 ppm in 1959) (Keeling and Whorf, 2001). Prior to 1900, [CO_2] fluctuated between 180-290 ppm for at least 400,000 years (Barnola et al., 1987; Jouzel et al., 1993). With respect to the recent and rapid increase in atmospheric [CO_2] during the 20th century, do invasive species show a stronger than expected response?

In contrast to future elevated CO_2 levels, less work has assessed the response of plants to the recent increase in atmospheric [CO_2], even though it is recognized that leaf and plant photosynthesis can be particularly sensitive to the low [CO_2] concentrations of the past (Polley et al., 1993). This is due in part to technical considerations since it is more difficult to remove CO_2 in experimental studies than it is to add it. Nevertheless, Sage (1995) summarized twelve studies over the range of pre-industrial relative to current levels. The estimated average relative biomass response between 270 and 380 ppm is approximately 29% (see Figure 3b, Sage, 1995). If this response is updated to include more recent reports, (i.e., wheat varieties Seri M82 and Yaqui, Mayeaux et al., 1997, *Albutilon theophrasti*, Dippery et al., 1995; Ward et al., 1999), the average relative growth response ($\pm$SD) is 33$\pm$11% for [CO_2] values between 250-270 ppm and 360-380 ppm.

Among invasive species however, the response to recent increases in atmospheric carbon dioxide is striking, rising by almost 90% on average, with field bindweed, Canada thistle and perennial sowthistle showing strong responses (Table 2). Although only a limited number of studies involving the response to recent [CO_2] increases are available, the response of noxious invasive species is about three times that of the reported average for other plant species over this range of CO_2 concentrations (see Sage, 1995). It could be argued that limitations of nutrients or water would negate the response of these species to recent atmospheric [CO_2] increases under field conditions; however, many of these species are associated with managed agronomic environments where water and nutrients would be optimal (see Patterson, 1995). In addition, for at least one noxious species, Canada thistle, nitrogen did not limit the relative growth response to recent [CO_2] changes (Ziska, 2003b).

Why is there such a strong response among invasive weeds to recent increases in atmospheric [CO_2]? It has been shown in numerous studies that belowground growth can show dramatic increases with increased [CO_2] (Rogers, Cure and Smith, 1986; Bernston and Woodward, 1992; Prior et al., 1994). Interestingly, of the most noxious weedy species listed by Skinner et al. (2000), many have a strong belowground root or rhizome system (e.g., Canada thistle, purple loosestrife, field bindweed, leafy spurge, Russian knapweed, whitetop, perennial sowthistle, quackgrass, dalmation toadflax) which can generate new stems from belowground structures. For a number of invasives, below ground biomass shows a strong response to recent increases in atmospheric carbon dioxide.

It is possible therefore that substantial below-ground sinks contributed to the large growth stimulation among noxious invasive weeds to recent [CO_2], providing a link between establishment and carbon dioxide responsiveness. However, at this time, carbon dioxide induced selection of propagation by vegetative means over floral reproduction remains only an intriguing possibility. The evolutionary role of increasing [CO_2] in the recent past cannot be fully elucidated from highly controlled experiments that examine single plant responses. While these types of data are useful in determining potential response, *in situ* responses will vary as a function of competition and environment with other factors antagonistic to the direction of selection (e.g., Etterson and Shaw, 2001).

RISING CO_2 AND NOXIOUS WEEDS: COMMUNITY LEVEL RESPONSES

Although there is a stronger than expected response of noxious weeds to both recent and projected increases in atmospheric carbon dioxide, the actual degree of photosynthetic or growth stimulation will vary by species and environment. While examining the impact of rising [CO_2] on individual noxious weeds provides a sense of potential increases in growth and reproduction, it is the aggregate response of noxious or invasive weeds within a plant community that should, empirically, provide the best estimate of whether rising [CO_2] is altering the success of these weedy invaders. For it is becoming increasingly evident that carbon dioxide, like other environmental resources, can act as a selecting factor within plant communities. That is, the response to either recent or projected changes in atmospheric [CO_2] is not uniform among plant species within a managed (e.g., Ziska 2001) or un-managed ecosystem. (Johnson et al., 1993; Phillips et al., 2002). Therefore, a key question remains: does rising [CO_2] preferentially favor the growth of noxious weeds among an assemblage of plants?

A number of scientists have attempted to delineate the specific response of plant functional groups to rising carbon dioxide, and it has been suggested that, theoretically, fast growing species under optimal conditions should show the greatest relative response to rising [CO_2] (Poorter et al., 1996). If this is true, then weeds, and noxious invasive weeds in particular, could be favored by increasing [CO_2].

Unfortunately, actual field data are rare, with only a handful of studies that have addressed this question. A comparison of the impact of increasing [CO_2] on an invasive, noxious weed, yellow star thistle, demonstrated a significant increase in biomass in monoculture , but a non-significant impact when yellow star thistle was grown within a grassland community (Dukes, 2002), suggesting that rising carbon dioxide did not stimulate the growth of this plant species preferentially. In contrast, work with honey mesquite (*Prosopis glandulosa*) and little bluestem (*Schizachyrium scoparium*) to recent changes in [CO_2], suggests that the woody invader, honey mesquite is preferentially stimulated by [CO_2] (Polley et al., 1994). Research on Japanese honeysuckle in a forest under-story also demonstrated a strong [CO_2] growth response and subsequent increase in percent cover (Belote et al., 2003). Experiments with a woody invasive (but not noxious) species in Switzerland, (*Prunus laurocerasus*) showed a stronger [CO_2] response relative to native trees (Hattenschwiler and Korner, 2003), also suggesting preferential growth of a non-native species. Finally, elevated [CO_2]

increased the productivity and invasive success of a noxious invasive rangeland weed associated with fire outbreaks (*Bromus madritensis*, spp. rubens) in an arid ecosystem (Smith et al., 2000). Overall, four of the five seminal studies suggest that rising levels of CO_2 can preferentially increase the growth of invasive plant species within a plant community.

CO_2 AND NOXIOUS WEEDS: WHY CAN'T WE SIMPLY CONTROL THESE PESTS?

It can be argued of course, that humans can control the establishment and success of invasive weeds either by mechanical, chemical or biological means. If noxious invasive weeds are becoming more of a problem, then sustained, concentrated management efforts are indeed needed. However, this assumes that the strong growth response to rising carbon dioxide by invasive, noxious weeds will not, by itself, alter the effectiveness of their management.

Studies are limited, but there is increasing evidence that rising CO_2 may reduce the effectiveness of weed control efforts. Canada thistle, for example, remains one of the worst agronomic weeds in North America (Skinner et al., 2000). Mechanical tillage, a common form of weed control, cuts and discs roots. But one of the common responses to rising [CO_2] is an increase in below-ground root growth relative to above-ground shoot growth (Ziska, 2002; Ziska, 2003b). Since Canada thistle is able to re-propagate from root segments as small as 0.8 mm in length (Donald, 1990), and since rising [CO_2]can double root growth relative to shoot growth in the field (Ziska et al., 2004), increasing tillage as a control measure would lead to additional plant propagation in a higher [CO_2] environment.

What about chemical control? There are an increasing number of studies (Ziska et al., 1999; Ziska and Teasdale, 2000) that demonstrate a decline in efficacy with rising [CO_2] for weeds including two noxious species, quackgrass and Canada thistle (Figure 1). In theory, rising [CO_2] could reduce foliar absorption of pesticides by reducing stomatal aperture or number; or, altering leaf or cuticular thickness. In addition, [CO_2] -induced changes in transpiration could limit uptake of soil applied pesticides. For weed control, timing of application could also be affected if elevated [CO_2] decreases the time the weed spends in the seedling stage (i.e., the time of greatest chemical susceptibility). For Canada thistle, increasing [CO_2] appears to have induced greater below-ground growth (roots), diluting the active ingredient of the herbicide and making chemical control less effective (Figure 1, Ziska et al., 2004). Biological control of weeds by natural or manipulated means is becoming increasingly recognized as an environmentally compatible pest management tool. However, such a strategy is also likely to be affected by increasing atmospheric [CO_2] and climatic change (Norris, 1982; Froud-Williams, 1996). Increasing carbon dioxide and potentially higher global temperatures could alter the efficacy of the bio-control agent by potentially altering the development, morphology and reproductive of the target pest. Direct effects of [CO_2] would also be related to changes in the ratio of C:N and potential negative interactions in the feeding habits and growth rate of herbivores (e.g., Lincoln et al., 1993).

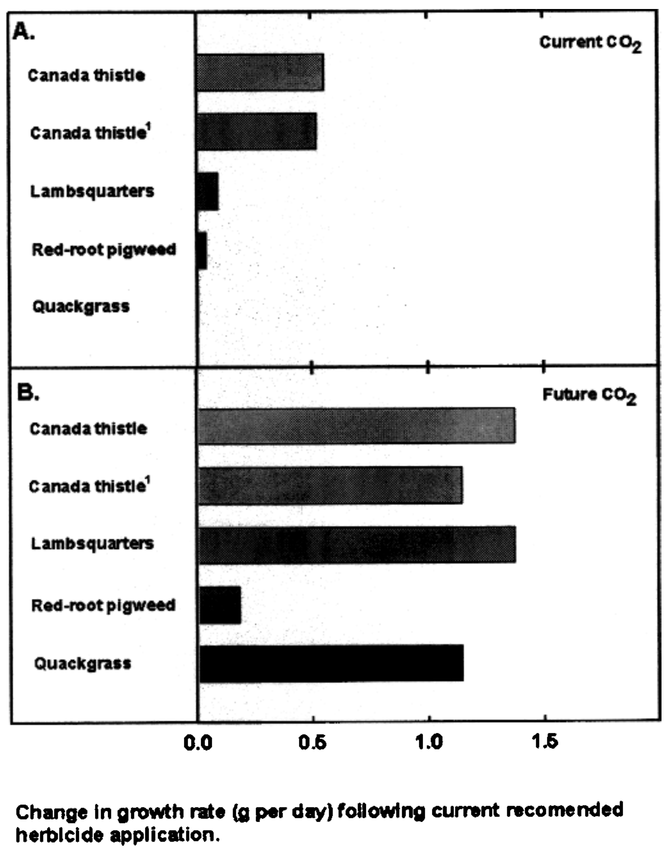

Figure 1 Change in growth rate (g dry matter per day) for agronomic weeds and noxious invasives when sprayed with recommended rates of herbicide at either (A) current levels of atmospheric carbon dioxide (360-400 ppm), or (B) future levels of atmospheric carbon dioxide (600-800) expected by the end of the century. Growth values for lambsquarters, red-root pigweed and quackgrass at current CO_2 levels were no different from zero (i.e. plant death), no plant deaths were recorded at future CO_2 levels. Herbicide was glyphosate in all cases except Canada thistle[1], which was sprayed with glufosinate. Data are from Ziska et al. 1999, Ziska and Teasdale 2000 and Ziska et al. 2004.

INVASIVE, NOXIOUS WEEDS: IGNORANCE IS *NOT* BLISS

Weeds then, are inextricably linked to human activities. As global commercial activity has increased, and trade barriers have fallen, long-distance dispersal of non-indigenous species has increased dramatically (di Castri, 1989). As a result, a small number of non-native species have become invasive / noxious and threaten managed plant communities as well as whole ecosystems (Vitousek and Walker, 1989; D'Antonion and Vitousek, 1992). As stated previously, exact environmental and economic costs are difficult to formulate but are estimated globally in the billions (Pimental et al., 1999)

Although the number of non-native species that become invasive is small, their numbers are growing. At the moment, more than 600 noxious/invasive weeds are recognized in North America, and hundreds more are recognized globally (Mooney and Hobbs, 2000). Recognition and assessment of other human activities that could, potentially, exacerbate their spread and success remains elusive. One such potential activity is the anthropogenic increase in the global concentration of carbon dioxide. Yet, incredibly, only a limited number of studies have specifically addressed how noxious plant species have responded to recent or future carbon dioxide increases, and only five studies have specifically examined whether rising CO_2 preferentially affects noxious weeds in plant communities. The dearth of current scientific studies prohibits a lack of consensus among the scientific community, with a subsequent lack of recognition of the problem among the public, and no clear understanding of the best strategies to resolve it. Clearly then, additional studies, particularly at the plant community level, must be initiated in the immediate future.

Such studies are crucial because even though the available data are limited, they suggest that, in fact, invasive weeds do show a strong response to $[CO_2]$, particularly recent $[CO_2]$ increases; and, what is more important, suggest that carbon dioxide may act to favor the growth of some invasive, noxious weeds for some plant communities in situ. Furthermore, initial data suggest that control of such weeds, either by mechanical, chemical or biological means may be impaired in a future, higher CO_2 environment.

CONCLUSIONS

Overall, we remain woefully ignorant of those human behaviors that contribute to the success of weedy invaders. This is evident not just with our current state of knowledge regarding $[CO_2]$ and noxious weeds, but with our knowledge (or lack thereof) regarding other human activities. For example, humans have dramatically altered the cycling of nitrogen on earth, with N deposition rates increasing more than tenfold over the last few decades (Wedin and Tilman, 1996). How has this additional resource altered the success of invasive weeds? Humans are also adding significant levels of ground level (tropospheric) ozone to the environment each year. Differential plant response to ozone has been shown to occur under field conditions (Krupa and Manning, 1988). Is the success of invasive weeds (and weeds in general) related to their greater ozone tolerance? With a current population of six billion, humans are changing the landscape and land use patterns on a global scale. What aspects of land use change are contributing to invasive species success?

Data are lacking on these and other global climatic issues of relevance regarding the long-term health and stability of global ecosystems. The ongoing increase in atmospheric carbon dioxide concentration is only one poorly understood factor that will almost certainly alter the growth, reproduction and location of invasive, noxious weeds. The environmental and economic costs of not understanding these impacts, and the appropriate control measures, may be substantial. Clearly, effective adaptation, mitigation and management strategies require a strong scientific consensus that accurately describes and predicts those human behaviors that contribute to the success of weedy invaders. Unfortunately, this information is incomplete, and as a consequence, current decisions may exacerbate future problems. To that end, it is hoped that this review will serve as a guide for interested researchers and policy makers in assessing the importance of rising atmospheric CO_2 to the biological success of invasive weeds; and will highlight key areas where additional information is needed.

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