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Allometric growth, disturbance regime, and dilemmas of controlling invasive plants: a model analysis

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Abstract Disturbed communities are observed to be more susceptible to invasion by exotic species, suggesting that some attributes of the invaders may interact with disturbance regime to facilitate invasion success. *Alternanthera philoxeroides*, endemic to South America, is an amphibious clonal weed invading worldwide. It tends to colonize disturbed habitats such as riparian zones, floodplain wetlands and agricultural areas. We developed an analytical model to explore the interactive effects of two types of physical disturbances, shoot mowing and root fragmentation, on biomass production dynamics of *A. philoxeroides*. The model is based on two major biological assumptions: (1) allometric growth of root (belowground) vs. shoot (aboveground) biomass and (2) exponential regrowth of shoot biomass after mowing. The model analysis revealed that the interaction among allometric growth pattern, shoot mowing frequency and root fragmentation intensity might lead to diverse plant 'fates'. For *A. philoxeroides* whose root allocation decreases with growing plant size, control by shoot mowing was faced with two dilemmas. (1) Shoot regrowth can be effectively suppressed by frequent mowing. However, frequent shoot mowing led to higher biomass allocation to thick storage roots, which enhanced the potential for faster future plant growth. (2) In the context of periodic shoot mowing, individual shoot biomass converged to a stable equilibrium value which was independent of the root fragmentation intensity. However, root fragmentation resulted in higher equilibrium population shoot biomass and higher frequency of shoot mowing required for effective control. In conclusion, the interaction between allometric growth and physical disturbances may partially account for the successful invasion of *A. philoxeroides*; improper mechanical control practices could function as disturbances and result in exacerbated invasion.

Keywords *Alternanthera philoxeroides* · Root fragmentation · Mowing · Plant invasion · Regrowth

Introduction

Management and control of invasive exotic species is a leading topic in invasion biology and applied ecology. Mathematical models have become an increasingly used tool to explore the most beneficial management strategies (e.g. Sharov and Liebhold

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1998; Taylor and Hastings 2004; Ruesink and Collada-Vides 2006; Raghu et al. 2007).

Understanding the mechanisms underlying invasion success is essential to making effective management strategies. Successful invasion depends both on the attributes of the invader (invasiveness) and the characteristics of the recipient community (invasibility) (Lonsdale 1999). Establishment and spread of plant invaders are generally facilitated in disturbed communities (Hierro et al. 2005). Disturbance can mediate competitive interaction between native and exotic species in ways that often favor the exotics (Minchinton and Bertness 2003; Leishman and Thompson 2005). Besides, disturbance often leads to increased resource supply into a community or decreased resource uptake by native plants, which provides niche opportunities for the establishment and proliferation of exotic plants (Davis et al. 2000). In terms of invasiveness, life history traits such as rapid regrowth (Sakai et al. 2001) and vegetative propagation (Lake and Leishman 2004) may interact with disturbance regime (i.e. type, intensity and frequency) to increase the potential for a plant to be invasive. Rapid regrowth enables plants to recover quickly from herbivory or mechanical damage (Hilbert et al. 1981); vegetative propagation allows biomass allocation to growth rather than to sexual reproduction, which may be an competitive advantage where disturbance increases resource availability (Lake and Leishman 2004).

Among the available weed control methods, mechanical control is considered to be a common approach used in agricultural systems due to the increasing health concerns of chemical control (Mack et al. 2000) and the possible nontarget effects of biological control (Louda et al. 2003). However, if mechanical control is viewed as a type of physical disturbance, it is reasonable to expect that improper control practices will lead to exacerbated invasion.

Alternanthera philoxeroides (Mart.) Griseb. (alligator weed), endemic to South America, is an amphibious clonal weed invading worldwide (Julien et al. 1995; Holm et al. 1997; Pan et al. 2007). Alligator weed has many general attributes of invasive weeds such as fast growth, vegetative propagation and broad ecological amplitude (Pan et al. 2007), and tends to invade disturbed habitats including riparian zones (Pan et al. 2006) and agricultural areas (Spencer and Coulson 1976). Biological control (release of its specialist natural enemies, e.g. *Agasicles hygrophila* and *Vogtia malloi*) has been successful in inhibiting *A. philoxeroides* growing in aquatic habitats, but failed to control its terrestrial populations (Julien and Chan 1992; Sainty et al. 1998). Mechanical methods, such as mowing and hoeing, are still widely used to contain *A. philoxeroides* in terrestrial environments.

In this study, we developed an analytical model to explore the interactive effects of two types of physical disturbances, shoot mowing and root fragmentation, on biomass production dynamics of *A. philoxeroides*. We addressed the following two questions. (1) How do plants with distinct allometric growth patterns respond to varying shoot mowing frequency and root fragmentation intensity? (2) Under which circumstances can shoot mowing be more effective in containing *A. philoxeroides*?

Materials and methods

Species characteristics

Thick storage roots (Fig. 1) play an important role in the life history of *A. philoxeroides*. In the introduced ranges, *A. philoxeroides* rarely produces viable seeds in the field and reproduces mainly by vegetative propagation with thick roots and stems (Pan et al. 2007; Geng et al. 2007a, b). In terrestrial environments, the large amount of root stores serves as the primary resource pool supporting population regeneration in early spring (Li and Xie 2002; Geng et al. 2006; Jia et al. 2007), supporting rapid regrowth after shoot damage caused by herbivory or physical disturbances. Thick root fragments can act as propagules for long-distance dispersal by flooding or human activities (e.g. soil transportation, dredging and road construction) (Pan et al. 2007). In addition, root allocation of *A. philoxeroides* changes adaptively in response to varying resource availabilities (Geng et al. 2006, 2007a).

Disturbance characteristics

The model considers the effects of the following two types of physical disturbances on *A. philoxeroides*: shoot mowing and root fragmentation. Shoot mowing is an extensively used mechanical method to control

Fig. 1 Clonal fragmentation of *Alternanthera philoxeroides* in terrestrial environments: thick storage roots and ramets (**a**), and buds sprouting from root fragments (**b**)

A. philoxeroides in agricultural and horticultural systems because root removal by digging is often onerous and could be detrimental to roots of the neighboring cultivated plants. Mowing is usually conducted periodically throughout a growing season to suppress the shoot regrowth. On agricultural lands, root fragmentation can be the result of various human activities, primarily the plowing and hoeing of soil at the beginning of a growing season. It usually results in the production of a large number of small root fragments (Fig. 1b) in vegetative propagule bank (Pan et al. 2007).

Modeling the disturbances and plant regrowth

The model is based on two major biological assumptions: (1) allometric growth of root (belowground) vs. shoot (aboveground) biomass and (2) exponential regrowth of shoot biomass after mowing (Fig. 2). Allometric growth has been extensively discussed and applied to quantify resource allocation and form-function relationship of plant species (West et al. 1999; Weiner 2004). The simplifying assumption of exponential growth was used because we were only concerned with the early vegetative growth in the context of periodic shoot mowing. Our empirical study showed that the biomass production of *A. philoxeroides* in terrestrial habitats (50 days after planting in early summer) can be well fitted by exponential model (Jia et al. 2007).

At individual level, the model was initiated with a single *A. philoxeroides* plant whose shoot biomass is S_0 and root biomass is R_0, at time 0 (Fig. 2). Shoot and root biomass are allometrically related (assumption 1):

$$R_0 = aS_0^b \tag{1}$$

where b ($b > 0$) is allometric scaling exponent, and a ($a > 0$) is allometric constant. We used varying R_0 to quantify the intensity of root fragmentation, i.e. smaller R_0 indicates higher fragmentation intensity. The allometric relationship of root vs. shoot biomass of *A. philoxeroides* was not affected by root propagule size (Pan 2005).

Subsequently, shoot biomass is governed by two recurrent processes: mowing and regrowth. Shoot mowing first occurs at time 0, and then recurs at T-day intervals (i.e. shoot mowing frequency is $1/T$). T was also used as the model's time-step (Fig. 2). After shoot mowing, an *A. philoxeroides* plant will lose most of its aboveground biomass, but the root-sprouting buds located near soil surface may be free from damage and serve as initial shoot biomass for the following regrowth (Pan et al. 2007) (Figs. 2 and 4). Pan (2005) reported that the number of buds sprouting from a buried root fragment increased linearly with root fragment biomass (Fig. 3). Although the linear relationship may not hold true when root biomass is much larger, we hold this assumption (i.e. bud number or biomass are proportional to root biomass) due to our focus on root fragmentation:

$$S_0' = kR_0 \tag{2}$$

where $S_0{}'$ is the bud biomass at the first shoot mowing (time 0), k is a constant representing the bud biomass per unit root biomass. After exponential regrowth (assumption 2), shoot biomass at the second mowing (time T), S_1, is

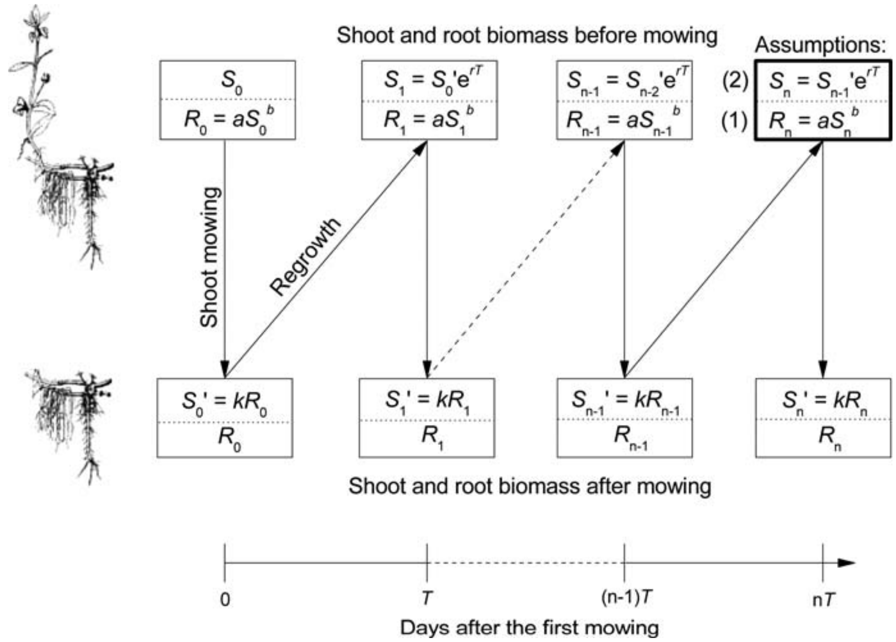
$$S_1 = S_0' \mathrm{e}^{rT} \tag{3}$$

where r is the mean relative growth rate of shoot biomass. Incorporating Eqs. 1 and 2 into Eq. 3 gives S_1 as a function of S_0:

$$S_1 = kaS_0^b \mathrm{e}^{rT} \tag{4}$$

After shoot mowing, plants will generally deviate from the allometric trajectory of root vs. shoot biomass, but will eventually follow it by shoot

Fig. 2 Diagrammatic representation of recurrent shoot mowing and regrowth. $\boldsymbol{R}_\mathbf{n}$, $\boldsymbol{S}_\mathbf{n}$, $\boldsymbol{S}_\mathbf{n}'$: individual root, shoot and bud biomass at the (n + 1) th mowing; ***a***: allometric constant; ***b***: allometric scaling exponent; ***r***: mean relative growth rate of shoot biomass; ***k***: bud biomass per unit root biomass; ***T***: shoot mowing interval



regrowth (McNaughton 1983; Reich et al. 1993). Depletion of root reserves could promote the returning process and lead to transitory decrease in root biomass (Fig. 4) (Thornton and Millard 1996; Ferraro and Oesterheld 2002). We specifically considered the situation that plants have returned back to the allometric trajectory before each mowing (i.e. T is greater than the time for returning to the allometric trajectory). Therefore after several steps of iteration, shoot biomass at the (n + 1) -th mowing (time nT), S_n, is given by

$$S_\mathrm{n} = kaS_{\mathrm{n}-1}^{b}\mathrm{e}^{rT} \tag{5}$$

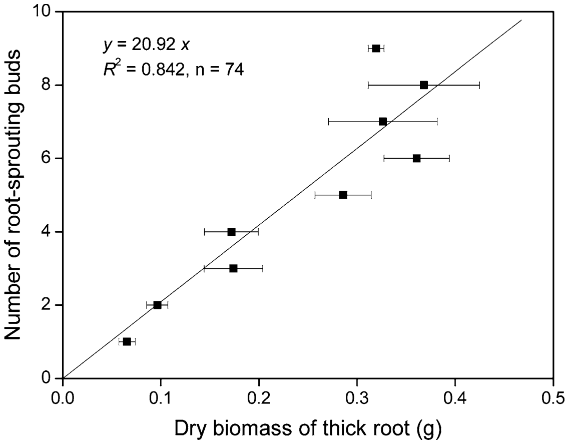


Fig. 3 Relationship between dry biomass of thick root and number of root-sprouting buds for *A. philoxeroides* in terrestrial environments (from Pan 2005)

The general form of Eq. 5 (see Appendix for derivation) is

$$\begin{cases} S_\mathrm{n} = (ka\mathrm{e}^{rT})^{\frac{1-b^\mathrm{n}}{1-b}} S_0^{b^\mathrm{n}} & \text{if } b \neq 1 \\ S_\mathrm{n} = (ka\mathrm{e}^{rT})^\mathrm{n} S_0 & \text{if } b = 1 \end{cases} \tag{6}$$

At population level, the model was initiated with an *A. philoxeroides* population containing N plants whose total shoot mass is P_0 and root mass is Q_0, at time 0. All plants were assumed to be uniform in size, so $P_0 = NS_0$ and $Q_0 = NR_0$. We used constant Q_0, independently of varying R_0 and N, to simulate the intensity of root fragmentation at population level, i.e. smaller R_0 or larger N indicates higher fragmentation intensity. The characteristics of shoot mowing and regrowth are the same as described at individual level. Therefore, population shoot biomass at the (n + 1) th mowing (time nT), P_n, is given by

$$P_\mathrm{n} = Nka\left(\frac{P_{\mathrm{n}-1}}{N}\right)^b \mathrm{e}^{rT} \tag{7}$$

The general form of Eq. 7 (see Appendix for derivation) is

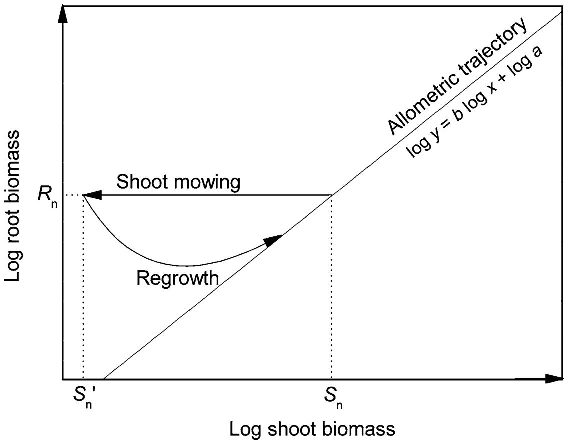


Fig. 4 Allometric trajectory of root vs. shoot biomass and regrowth of *A. philoxeroides* after shoot mowing. After shoot mowing, an *A. philoxeroides* plant will lose most of its aboveground biomass, and deviate from the allometric trajectory of root vs. shoot biomass. However, root-sprouting buds located near the soil surface may be free from damage and serve as initial shoot biomass for the following regrowth. Plants will follow the allometric trajectory by shoot regrowth, and depletion of root reserves could promote the returning process and lead to transitory decrease in root biomass

$$\begin{cases} P_{\mathrm{n}} = N^{1-b^{\mathrm{n}}}(kae^{rT})^{\frac{1-b^{\mathrm{n}}}{1-b}}P_0^{b^{\mathrm{n}}} & \text{if } b \neq 1 \\ P_{\mathrm{n}} = (kae^{rT})^{\mathrm{n}}P_0 & \text{if } b = 1 \end{cases} \tag{8}$$

For *A. philoxeroides* plants grow in the field (with abundant resources) in early summer (average daily temperature is about 20°C), the approximate parameter values are $a = 0.44 \pm 0.019$, $b = 0.73 \pm 0.024$, $r = 0.12 \pm 0.004$ (mean ± SE) (Jia et al. 2007) and $k \leq 0.1$ (unpublished data).

Model analysis, simulations and results

Regrowth isoline and conditions for effective control

By a series of algebraic manipulations (see Appendix for more details), we can obtain an equation for $S_{\mathrm{n}} = S_{\mathrm{n}-1}$ and $P_{\mathrm{n}} = P_{\mathrm{n}-1}$:

$$ka^{\frac{1}{b}}e^{rT}R_0^{\frac{b-1}{b}} = 1 \tag{9}$$

After holding k, a, b and r constant in Eq. 9, a regrowth isoline (Fig. 5a–c) can be defined by

$$T^* = \frac{(1-b)\ln R_0 - b\ln k - \ln a}{br} \tag{10}$$

or alternatively, by

$$R_0^* = (k^b a e^{brT})^{\frac{1}{1-b}} \quad \text{if } b \neq 1 \tag{11}$$

where T^* and $R_0{}^*$ are the required shoot mowing interval or root fragmentation intensity for keeping shoot biomass stationary over time. The regrowth isoline is qualitatively affected by the allometric scaling exponent (b): when $0 < b < 1$, T^* increases with increasing R_0, or $R_0{}^*$ increases with increasing T (Fig. 5a); when $b > 1$, T^* decreases with increasing R_0, or $R_0{}^*$ decreases with increasing T (Fig. 5b); when $b = 1$, T^* is independent of R_0, and the isoline is parallel to the R_0 axis (i.e. there is no $R_0{}^*$) (Fig. 5c). Additional model analyses indicate that k, a and r have no qualitative effects on the isoline (not shown).

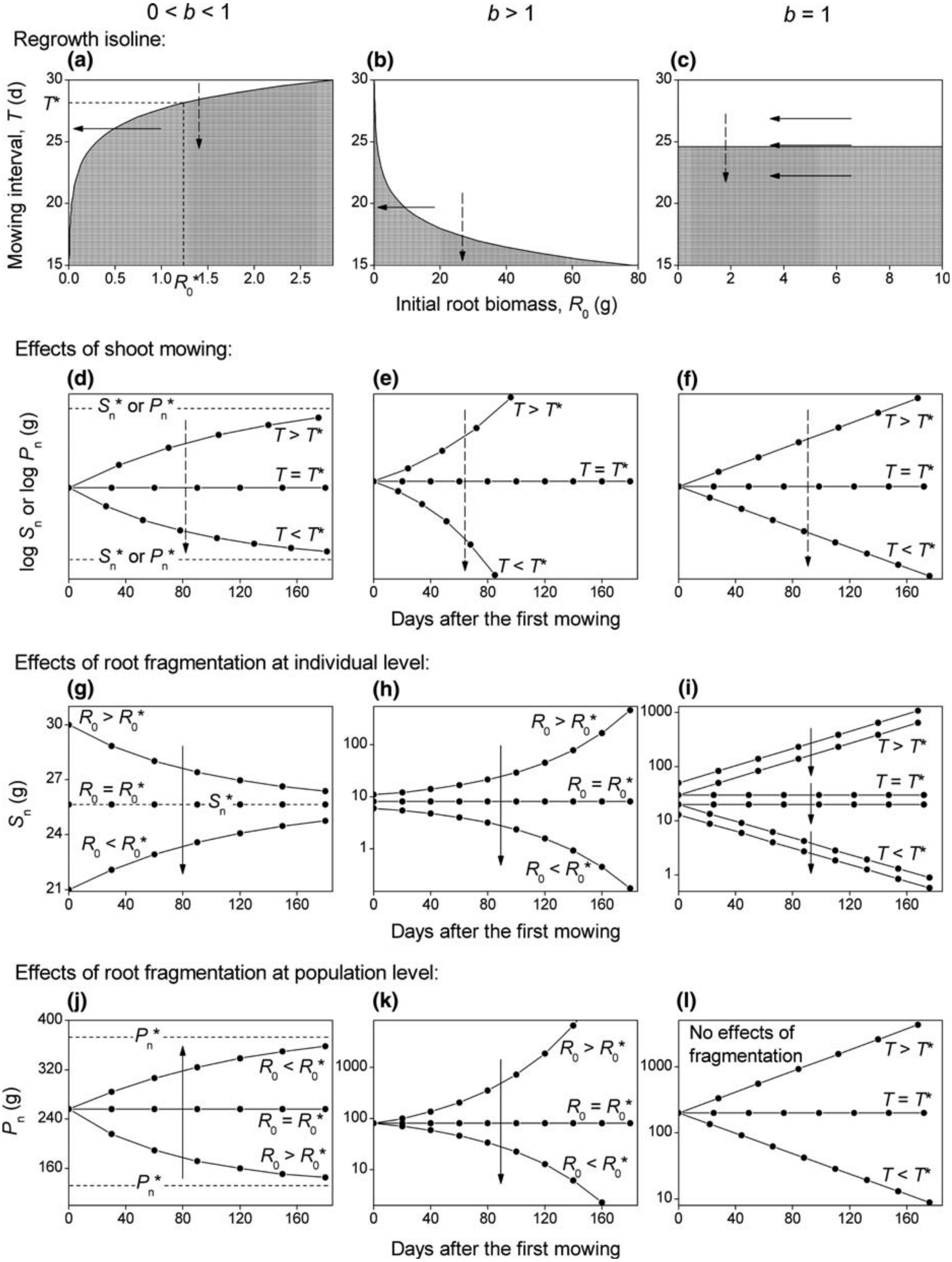
We employed $S_{\mathrm{n}} < S_{\mathrm{n}-1}$ and $P_{\mathrm{n}} < P_{\mathrm{n}-1}$ to be the criteria for effective reduction of shoot biomass at individual and population levels, respectively. Decrease of shoot biomass also implies decrease of root biomass because they are allometrically related (see assumption 1). Under the circumstance of constant root fragmentation intensity (constant R_0):

$$\begin{cases} S_{\mathrm{n}} > S_{\mathrm{n}-1}, P_{\mathrm{n}} > P_{\mathrm{n}-1} & \text{if } T > T^* \\ S_{\mathrm{n}} < S_{\mathrm{n}-1}, P_{\mathrm{n}} < P_{\mathrm{n}-1} & \text{if } T < T^* \end{cases} \tag{12}$$

(Figures 5a–f). Therefore, plant regrowth can be effectively suppressed when shoot mowing is performed frequently, and this pattern is independent of b. However, under the situation of constant shoot mowing frequency (constant T), the effects of root fragmentation depend greatly on b:

$$\begin{cases} 0 < b < 1 \begin{cases} S_{\mathrm{n}} > S_{\mathrm{n}-1}, P_{\mathrm{n}} > P_{\mathrm{n}-1} & \text{if } R_0 < R_0^* \\ S_{\mathrm{n}} < S_{\mathrm{n}-1}, P_{\mathrm{n}} < P_{\mathrm{n}-1} & \text{if } R_0 > R_0^* \end{cases} \\ b > 1 \begin{cases} S_{\mathrm{n}} > S_{\mathrm{n}-1}, P_{\mathrm{n}} > P_{\mathrm{n}-1} & \text{if } R_0 > R_0^* \\ S_{\mathrm{n}} < S_{\mathrm{n}-1}, P_{\mathrm{n}} < P_{\mathrm{n}-1} & \text{if } R_0 < R_0^* \end{cases} \end{cases} \tag{13}$$

(Figures 5a, b, g, h, j and k). When $b = 1$, root fragmentation only reduces the absolute plant size (S_{n}), but does not change the regrowth trend (Fig. 5c and i), and has no effect on population shoot biomass (P_{n}) (Fig. 5l).


0 < b < 1
b > 1
b = 1
Regrowth isoline:
(a)
(b)
(c)
Mowing interval, T (d)
T*
R0*
Initial root biomass, R0 (g)
Effects of shoot mowing:
(d)
(e)
(f)
log Sn or log Pn (g)
Sn* or Pn*
T > T*
T = T*
T < T*
Days after the first mowing
Effects of root fragmentation at individual level:
(g)
(h)
(i)
Sn (g)
R0 > R0*
R0 = R0*
R0 < R0*
Sn*
Effects of root fragmentation at population level:
(j)
(k)
(l)
Pn (g)
Pn*
No effects of fragmentation

◀ **Fig. 5** Effects of shoot mowing and root fragmentation on biomass production dynamics of *A. philoxeroides*. $\boldsymbol{T^*}$, $\boldsymbol{R_0^*}$: required shoot mowing interval and root fragmentation intensity for keeping shoot biomass stationary over time; $\boldsymbol{S_n^*}$, $\boldsymbol{P_n^*}$: equilibrium individual and population shoot biomass; other symbols are described in Figure 2. Dash arrows represent the increasing shoot mowing frequency; solid arrows represent the increasing root fragmentation intensity. Grey areas below the regrowth isolines represent the circumstances under which biomass decreases with time. Parameter values used in simulations: $a = 0.25$; $b = 0.75$, 1.33 and 1; $r = 0.15$; $k = 0.1$

Equilibrium shoot biomass

The model has a positive asymptotic equilibrium when $0 < b < 1$, the equilibrium individual shoot biomass, $S_n{}^*$, is

$$S_n^* = \lim_{n\to\infty} S_n = \left(kae^{rT}\right)^{\frac{1}{1-b}} \tag{14}$$

and the equilibrium population shoot biomass, P_n^*, is

$$P_n^* = \lim_{n\to\infty} P_n = N\left(kae^{rT}\right)^{\frac{1}{1-b}} \tag{15}$$

S_n^* increases with the shoot mowing interval (T), but is independent of the root fragmentation intensity (R_0) (Fig. 5d and g); however, $P_n{}^*$ increases with both the shoot mowing interval (T) and the root fragmentation intensity (N) (Fig. 5d and j). The model has no asymptotic equilibrium when $b \geq 1$.

Discussion

Our results show that plant regrowth dynamics depended on the interaction among allometric growth pattern, shoot mowing frequency and root fragmentation intensity. This interaction might lead to diverse plant 'fates': sufficiently frequent mowing (i.e. $T < T^*$, constant R_0) can be effective in suppressing plant regrowth (Fig. 5d–f); at population level, higher intensity of root fragmentation (i.e. $R_0 < R_0{}^*$, constant T) is advantageous to control when $b > 1$, but is disadvantageous to control when $0 < b < 1$ (Fig. 5j and k). According to our empirical study, root allocation of *A. philoxeroides* decreased with growing plant size in terrestrial environments (i.e. $0 < b < 1$) (Jia et al. 2007). Under this allometric relationship, control of *A. philoxeroides* by shoot mowing is faced with the following two dilemmas.

Dilemma 1: mowing frequency: reduced biomass vs. elevated root allocation

It was not surprising that shoot biomass can be reduced successfully by applying frequent mowing (Wilson and Clark 2001; Li et al. 2004). Nevertheless, smaller plants indicated a higher root allocation when $0 < b < 1$ (see Eq. 1). Actually, several studies have shown that clonal plants might respond to repeated shoot mowing by increasing belowground growth or allocation (e.g. root, rhizome) (Stoll et al. 1998; Li et al. 2004). *A. philoxeroides* also regrows with a higher root to shoot ratio after shoot removal (Schooler et al. 2007; Wilson et al. 2007). Elevated root allocation poses a latent dilemma in mechanical control: by regrowing with a higher root to shoot ratio, *A. philoxeroides* plants would suffer much less biomass loss in the subsequent shoot mowing (Wilson et al. 2007). Furthermore, the large amount of resources stored in thick roots can buffer plants against unfavorable growing conditions (Iwasa and Kubo 1997; Suzuki and Stuefer 1999) and enables *A. philoxeroides* to recover rapidly from shoot damage, thus increases its potential for further persistence.

Dilemma 2: root fragmentation: converged individual biomass vs. elevated population biomass

Although our model predicted that in the case of repeated mowing the individual shoot biomass of *A. philoxeroides* eventually converged to an equilibrium value which is independent of the root fragmentation intensity (Fig. 5g), the population shoot biomass can achieve a higher equilibrium value by root fragmentation (Fig. 5j). Like *A. philoxeroides*, many invasive plants impose negative impacts on native communities by their dense monocultures that virtually exclude many native plants (Mack et al. 2000). Therefore the equilibrium population size or biomass production should be another important measurement of control efficiency, i.e. higher equilibrium population biomass implies low control efficiency.

In addition, invasion success of *A. philoxeroides* could be greatly facilitated by root fragmentation for several reasons. Firstly, the direct consequence of root fragmentation might be the production of large numbers of vegetative propagules, hence a greater possibility of increased recruitment into populations

(Wright and Davis 2006) and a greater opportunity for long-distance dispersal (Pan et al. 2007). Secondly, root fragmentation led to higher frequency of shoot mowing required for effective control (Fig. 5a and j). Thirdly, by yielding many small plants, root fragmentation can also result in enhanced root allocation, which enables *A. philoxeroides* to regrow rapidly.

All the benefits that clonal species could gain from vegetative fragmentation are based on the prerequisites that the fragment survivorship is high and the density-dependent effects are minimal (Wright and Davis 2006). Our previous studies show that the sprouting rate of root fragments for *A. philoxeroides* reached 100% independently of the root fragment size (1–6 cm in length) and burial depth (3–15 cm below the soil surface). Furthermore, although there was density-dependent mortality, the ramets emerged from root fragments had survivorship of nearly 100% at low planting density (about 100 root fragments per m^2) and maintained nearly 90% at extremely high density (about 760 root fragments per m^2) (Pan 2005). So it is conceivable that root fragmentation can facilitate population increase of *A. philoxeroides*.

Management implications

Our findings have important implications for management and control of *A. philoxeroides* in terrestrial environments. (1) Mechanical control such as shoot mowing needs to be performed as frequently as possible so long as the costs are acceptable. (2) Fragmentation of thick roots should be avoided in the processes of mechanical control and other cultivation activities. (3) If fragmentation has occurred, as many as root fragments should be removed from soil and then incinerated to reduce the vegetative propagule bank, hence the recruitment into populations.

Our study focused on the effects of two types of anthropogenically physical disturbances on biomass production of *A. philoxeroides*. However, this simple model and its underlying mechanisms could work for other invasive clonal plants (e.g. *Solidago canadensis* and *Spartina alterniflora*) and could also be useful in exploring the effects of other types of disturbances (e.g. flooding, grazing and herbivory).

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Appendix 1: Derivation of the general equations and the condition for $S_\mathrm{n} = S_\mathrm{n-1}$ and $P_\mathrm{n} = P_\mathrm{n-1}$

At individual level

Individual shoot biomass at the first mowing (time 0, see Fig. 2) is S_0. According to Eq. 5, shoot biomass at the second mowing (time T), S_1, is

$$S_1 = kaS_0^b\mathrm{e}^{rT}$$

Similarly, at the third mowing (time $2T$), S_2 is

$$S_2 = kaS_1^b\mathrm{e}^{rT} = k^{b+1}a^{b+1}S_0^{b^2}\mathrm{e}^{(b+1)rT}$$

and at the fourth mowing (time $3T$), S_3 is

$$S_3 = kaS_2^b\mathrm{e}^{rT} = k^{b^2+b+1}a^{b^2+b+1}S_0^{b^3}\mathrm{e}^{(b^2+b+1)rT}$$

Conclusively, individual shoot biomass at the (n + 1) th mowing (time nT), S_n, is given by

$$\begin{cases} S_\mathrm{n} = (ka\mathrm{e}^{rT})^{\frac{1-b^\mathrm{n}}{1-b}}S_0^{b^\mathrm{n}} & \text{if } b \neq 1 \\ S_\mathrm{n} = (ka\mathrm{e}^{rT})^\mathrm{n}S_0 & \text{if } b = 1 \end{cases}$$

Now the condition under which $S_\mathrm{n} = S_\mathrm{n-1}$ turns out to be equal to

$$\begin{cases} (ka\mathrm{e}^{rT})^{\frac{1-b^\mathrm{n}}{1-b}}S_0^{b^\mathrm{n}} = (ka\mathrm{e}^{rT})^{\frac{1-b^{\mathrm{n}-1}}{1-b}}S_0^{b^{\mathrm{n}-1}} & \text{if } b \neq 1 \\ (ka\mathrm{e}^{rT})^\mathrm{n}S_0 = (ka\mathrm{e}^{rT})^{\mathrm{n}-1}S_0 & \text{if } b = 1 \end{cases}$$

This expression can be simplified to

$$ka\mathrm{e}^{rT}S_0^{b-1} = 1$$

After incorporating Eq. 1 into the above equation, we can obtain Eq. 9:

$$ka^{\frac{1}{b}}\mathrm{e}^{rT}R_0^{\frac{b-1}{b}} = 1$$

At population level

Population shoot biomass at the first mowing (time 0) is P_0. According to Eq. 7, population shoot biomass at the second mowing (time T), P_1, is

$$P_1 = Nka\left(\frac{P_0}{N}\right)^b\mathrm{e}^{rT} = N^{1-b}kaP_0^b\mathrm{e}^{rT}$$

Similarly, at the third mowing (time $2T$), P_2 is

$$P_2 = Nka\left(\frac{P_1}{N}\right)^b e^{rT} = N^{1-b^2}k^{b+1}a^{b+1}P_0^{b^2}e^{(b+1)rT}$$

and at the fourth mowing (time $3T$), P_3 is

$$\begin{aligned} P_3 &= Nka(\frac{P_2}{N})^b e^{rT} \\ &= N^{1-b^3}k^{b^2+b+1}a^{b^2+b+1}P_0^{b^3}e^{(b^2+b+1)rT} \end{aligned}$$

In conclusion, the population shoot biomass at the (n + 1) th mowing (time $\mathrm{n}T$), P_n, is given by

$$\begin{cases} P_\mathrm{n} = N^{1-b^\mathrm{n}}(kae^{rT})^{\frac{1-b^\mathrm{n}}{1-b}}P_0^{b^\mathrm{n}} & \text{if } b \neq 1 \\ P_\mathrm{n} = (kae^{rT})^\mathrm{n}P_0 & \text{if } b = 1 \end{cases}$$

Now the condition under which $P_\mathrm{n} = P_{\mathrm{n}-1}$ is equal to

$$\begin{cases} N^{1-b^\mathrm{n}}(kae^{rT})^{\frac{1-b^\mathrm{n}}{1-b}}P_0^{b^\mathrm{n}} = N^{1-b^{\mathrm{n}-1}}(kae^{rT})^{\frac{1-b^{\mathrm{n}-1}}{1-b}}P_0^{b^{\mathrm{n}-1}} & \text{if} b \neq 1 \\ (kae^{rT})^\mathrm{n}P_0 = (kae^{rT})^{\mathrm{n}-1}P_0 & \text{if} b = 1 \end{cases}$$

This expression can be simplified to

$$kae^{rT}(\frac{P_0}{N})^{b-1} = 1$$

further to

$$kae^{rT}S_0^{b-1} = 1$$

After incorporating Eq. 1 into the above equation, we arrive at Eq. 9 again:

$$ka^{\frac{1}{b}}e^{rT}R_0^{\frac{b-1}{b}} = 1$$

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