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Effect of Root Fragment Length and Planting Depth on Clonal Establishment of Alligatorweed

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ABSTRACT

Alligatorweed (*Alternanthera philoxeroides* [Mart.] Griseb) is commonly abundant in open disturbed riparian zones in south China. Based on field observations, roots of alligatorweed are often fragmented into different sizes and buried at various depths in the soil following disturbances such as flooding and mechanical control. To gain knowledge about the regeneration of alligatorweed from root fragments following mechanical control, the viability of root fragments was studied in pots. Roots were cut into three lengths (1, 3, and 6 cm) and planted at depths of 3, 7, and 15 cm in pots. All root fragments sprouted at least one ramet 33 days after planting. The time of emergence was delayed by greater soil depth but was not affected by tuber size or by the interaction of tuber size and soil depth. The emergence rate (depth/mean emergence time, cm day^{-1}) increased with planting depth. Ramet number per root increased with root size but was not affected by soil depth or by the interaction of root size and soil depth. Although the dry mass and leaf area of alligatorweed increased with increasing tuber size and reduced

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with planting depth significantly, these treatments had no effect on the root:shoot ratio. These results suggest that mechanical control of alligatorweed is of low efficacy if root fragments are left within 15 cm of the soil surface.

Key words: *Alternanthera philoxeroides*, biomass allocation, emergence, riparian zones.

INTRODUCTION

Riparian zones, the interfaces between terrestrial and aquatic ecosystems, are particularly susceptible to invasion by exotic species because of the high frequency disturbances and readily available soil resources (Planty-Tabacchi et al. 1996, Hood and Naiman 2000). Aquatic weed species have the potential to spread by seed and/or clonal fragments (e.g., tubers, stolons, or rhizomes). In most cases, however, clonal growth predominates in invasive aquatic weeds and seeds contribute relatively little to their spread (Alpert et al. 2000). In riparian habitats, disturbances such as flooding and cutting often produce vegetative fragments that may be buried in the sediment at different depths (Bourdot 1984, Dietz et al. 1999, Smith and Walters 1999, Fernandez 2003, Shen et al. 2005). Thus, clonal fragment size and burial depth may affect ramet emergence and subsequent growth in these fragments.

The reestablishment phase of a weed is crucial because it determines the effective recruitment of new ramets during the early period of weed population establishments (Radosevich et al. 1997). Weed control decisions are commonly based on density of seedlings or other attributes of the weed population, such as spatial distribution and emergence period (Bourdot 1984, Fernandez 2003).

We studied the clonal establishment behavior (ramet emergence and growth and biomass allocation) of alligatorweed root fragments. We chose root fragments rather than other vegetative propagules because alligatorweed has a very dense root system concentrated in the upper 20 cm of the soil, and most of the belowground dry biomass (>70%) is involved in storage (Jia et al. 2008). Buds and ramets regenerated from massive storage roots have played an important role in formation of local dense populations of alligatorweed (Pan et al. 2007). In earlier successional habitats, alligatorweed generally forms individual patches (Figure 1a), which consists of clusters of daughter ramets on a fragment of mother storage root (Figure 1b). The size of patches varies widely, with sometimes as much as a 20-fold difference in patch diameter (Pan et al. 2006). Thus, the population dynamics of alligatorweed can be influenced by the size of mother storage roots and its establishment habitats after disturbance. The objectives of this research were to determine if alligatorweed ramet emergence is affected by root fragment size and planting depth and to determine if ramet growth and biomass allocation are affected by root fragment size and planting depth. The root fragment lengths and planting depths used in this research were intended to simulate the different fragment sizes and burial depths that would occur as a result of disturbances such as flooding or mechanical control.

MATERIALS AND METHODS

We excavated storage roots of alligatorweed from the riparian dunes in Zhuji (Zhejiang Province, China) on 27 April 2004 and transported them to the laboratory in polyethylene bags. All fine adventitious roots were washed and removed, and storage roots (3-5 mm dia) were cut into 1-, 3-, or 6-cm fragments and germinated in the dark at 15 to 20 C. After 2 weeks, root fragments with at least one vigorous bud were selected for transplanting into 20-cm diameter by 30-cm deep plastic pots containing 3.5 L of a 3:1 mixture of loamy soil and silica sand. One root fragment was planted horizontally into each pot at one of three depths (3, 7, or 15 cm) with the sprouting bud oriented upward. Three root fragment lengths and three burial depths were applied in a complete factorial design. Root fragments were randomly assigned to one of the nine treatment combinations, and each treatment was replicated five times. Peter's fertilizer (N-P-K = 20-20-20; Scotts Co., USA) was initially applied as base nutrients (5 g per pot), and pots were fertilized weekly with 4 g Peter's fertilizer per pot. Watering by hand was performed every other day to keep the mixture moist. All pots were grown in a greenhouse (25-36 C, 14:10 light:dark) at Fudan University, Shanghai.

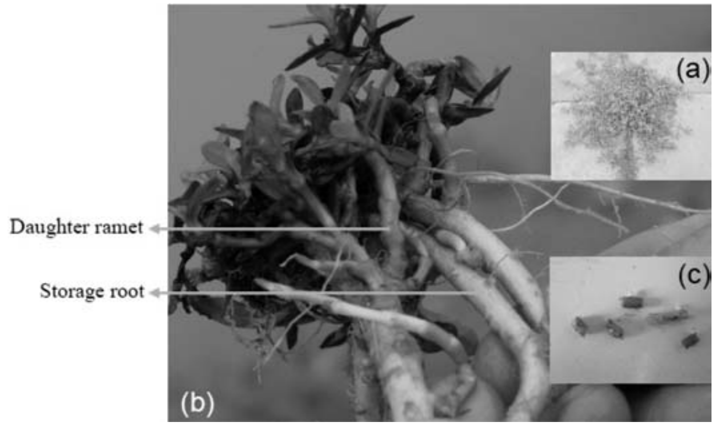

Figure 1. Clonal growth of alligatorweed: (a) a plant patch; (b) cluster of daughter ramets on storage root; (c) buds on root fragments.

Ramet emergence was recorded daily, and the last ramet sprouted 33 days after planting (DAP). The number of emerged ramets per root fragment was counted 56 DAP, and stem length (the length of the longest ramet) was measured from the soil surface to the tip of the apical meristem. Each plant was separated into leaves, stems, and roots (belowground biomass). The original root fragment was not included in determination of belowground biomass. Leaf area of plants generated from each root fragment was determined using an electronic planimeter (LI 3100, Li-Cor, Lincoln, NE, USA), and dry biomass of plant segments was measured after the material had been oven dried (80 C, 48 h).

Emergence rate was regressed as a function of DAP using a logistic regression model:

$$ER = \frac{1}{Y^{-1} + a \cdot b \cdot DAP}$$

where ER = alligatorweed emergence rate (%); and Y, a, and b = regression model parameters. The DAP for 50% of root fragments was calculated as:

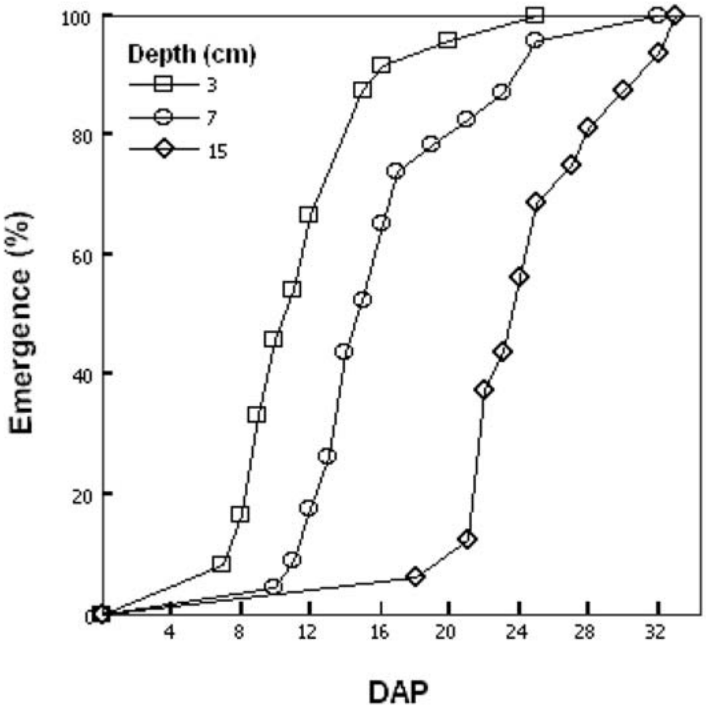

Figure 2. The effect of planting depth on the emergence dynamics of alligatorweed ramets regenerated from root fragments with days after planting (DAP).

$$DAP_{50\%} = (\ln Y - \ln a) / \ln b$$

where Y = 100%.

All dependent variables were log-transformed where necessary to meet assumptions of normality and homogeneity of variance. The effect of the initial root fragment size was included as block, but it is not reported because it was not significant in any analysis. The growth data (dry biomass, leaf area, stem length, and the number of ramets per root fragment) were analyzed using a two-way analysis of variance (ANOVA) to test the effect of root fragment size and burial depth on the variables.

RESULTS AND DISCUSSION

Ramets emerged from root fragments within 33 DAP (Figure 2). The emergence time was affected by planting depth ($F_{2, 36}$ = 30.32, P < 0.001) but not by root fragments size ($F_{2, 36}$ = 2.18, P = 0.12) or depth x size interaction ($F_{4, 36}$ = 0.78, P = 0.54), which is consistent with the findings of Shen at al. (2005). Because emergence potential was insensitive to root size, we pooled the data across the three sizes to test the effect of burial depth on emergence. There was a significant logistic relationship between emergence time and the emergence percentage of root fragments, and the times needed for 50% of emergence were 11, 16, and 24 days at 3 cm, 7cm, and 15 cm depth, respectively (Table 1). But the mean emergence time per unit depth (days/cm) decreased with planting depth (3.7 → 2.3 → 1.6 days/cm). The more rapid emergence rate (days/cm) at greater planting depths may be a result of increasing soil temperatures at greater depths (Guo et al. 2001). The rapid sprouting and emergence of alligatorweed following disturbance confirmed that the vast majority of the buds on roots were viable and under an environmentally imposed quiescence.

Both root size and planting depth had a significant effect on ramet growth (Figure 3; Table 2). Generally, the larger the fragment, the larger the regenerated ramets; the greater the depth of planting, the smaller the regenerated ramets, irrespective of which parameter (i.e., total mass, shoot biomass, root biomass, or total leaf area) was measured (Figure 3). Stem length decreased with increasing planting depth (Figure 3) but was unaffected by root size or depth x root size interaction (Table 2). Larger roots generated more ramets per root fragment (Figure 3), but burial depth or depth x root size interaction did not affect the number of ramets produced per root (Table 2). Depth x size interactions generally had no effect on ramet growth (Table 2).

Although root fragment size and planting depth significantly affected alligatorweed growth (Tables 2 and 3), these treatments had no effect on partitioning of dry mass between root and shoot (Figure 4; Table 2). This result suggests that the differences in allocation patterns of alligatorweed under varying disturbance conditions are largely due to allometric growth ("apparent plasticity," McConnaughay and Coleman 1999). Such firm responses can enhance plant reproductive effort at the population level, especially in monocultures (Weiner 2004).

Storage of resources is a widespread phenomenon in clonal species and can be understood as a safety measure against temporal changes in the growing conditions of plants; storing carbohydrates for later use enables plants to rapidly resume growth and reproduction (Suzuki and Steufer. 1999). The results of this study suggest that reestablishment from root fragments is not affected by fragmentation disturbance, which indicates that the efficacy of mechanical control of alligatorweed may be low (Jia et al. 2009). Our results also support the hypothesis that fragmen-

TABLE 1. EFFECT OF PLANTING DEPTH ON EMERGENCE TIME FOR ROOT FRAGMENTS OF *ALLIGATORWEED*. THE EMERGENCE TIME FOR 50% OF SPROUTING WAS ESTIMATED FROM THE LOGISTIC REGRESSION BETWEEN ACCUMULATIVE EMERGENCE RATE AND EMERGENCE TIME. VALUES IN PARENTHESES REPRESENT STANDARD ERRORS (SE).

	Emergence time (DAP, days after planting)				Logistic regression parameters				
Depth	First	Last	Mean	50%	*a*	*b*	*df*	*P*	R^2
3 cm	5	21	10.0 (0.8)	11.1	1.70 (0.68)	0.63 (0.02)	8	<0.001	0.97
7 cm	12	27	17.8 (1.1)	16.0	5.76 (2.76)	0.67 (0.02)	11	<0.001	0.95
15 cm	18	33	24.5 (1.0)	24.0	1553.4 (283.0)	0.61 (0.04)	9	<0.001	0.85

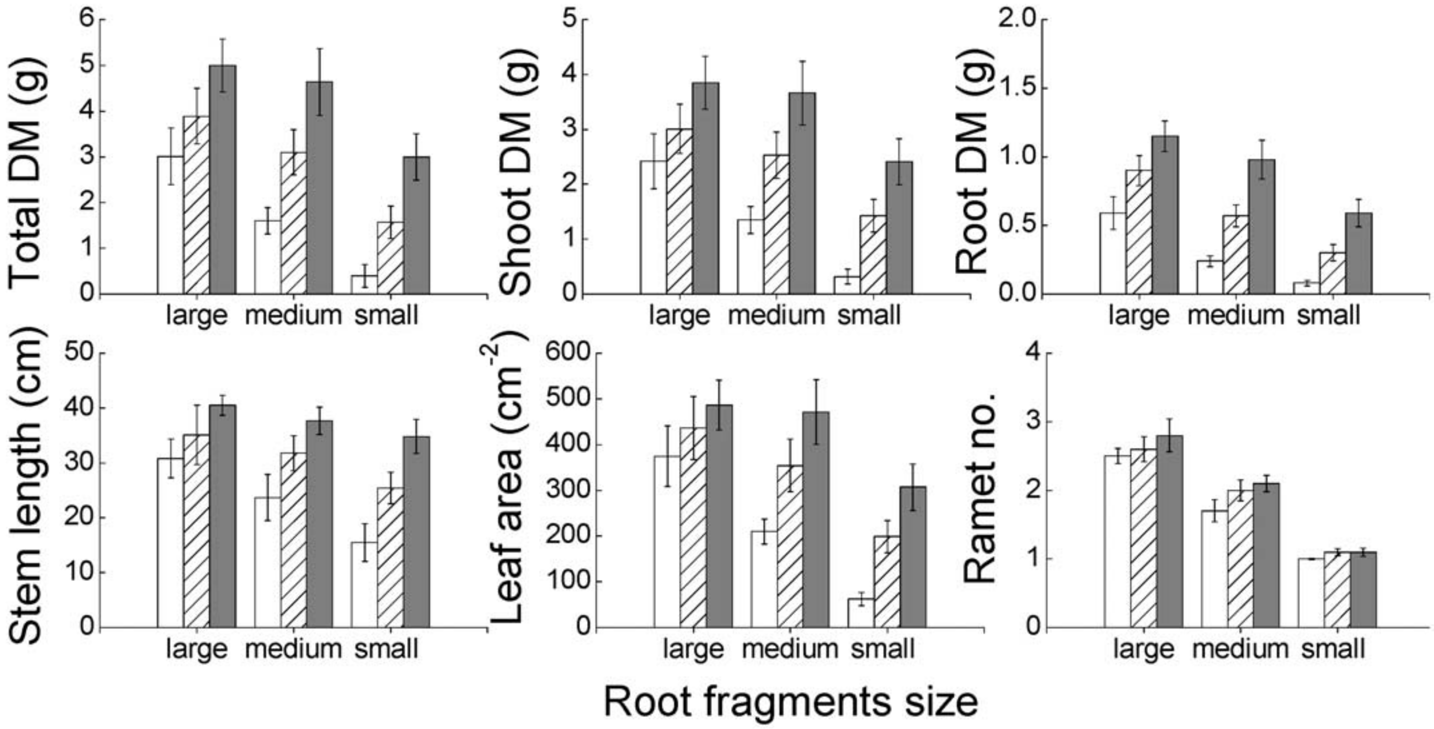

Figure 3. Effects of root size and planting depth on growth of alligatorweed. Means and 1SE (n = 5) are shown. Plant depth: 3 cm white bar; 7 cm diagonal bar; 15 cm dark bar.

tation is an effective propagation mechanism that contributes to the spread of invasive weeds (Smith and Walters 1999, Pan et al. 2007, Jia et al. 2009).

Also note that alligatorweed fragments used in this study were maintained under favorable growing conditions. Under natural field conditions, fragments could free-float for extended periods of time, potentially lowering the viability of individual fragments. Future research needs to determine the effect of damage to free-floating alligatorweed fragments on fragment viability.

TABLE 2. *F*-VALUES OF A TWO-WAY ANALYSIS OF VARIANCE (ANOVA) ON PLANT CHARACTERISTICS OF *ALLIGATORWEED* REGENERATED FROM THREE ROOT FRAGMENT SIZES (1, 3, AND 6 CM LENGTH) PLANTED AT THREE DEPTHS (3, 7, AND 15 CM). DEGREES OF FREEDOM IN THE MODEL WERE: ROOT FRAGMENT SIZE (2), DEPTH (2), AND SIZE X DEPTH (4). SIGNIFICANCE IS DEFINED AS: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source	Root fragment size	Depth	Size × depth
Total mass (g)	8.05**	18.43***	0.79
Shoot mass (g)	8.08**	18.09***	0.84
Leaf mass (g)	8.87**	15.73***	0.99
Stem mass (g)	8.50**	20.57***	0.94
Root mass (g)	8.96**	14.58***	0.68
Leaf area (cm^2)	7.36**	11.66***	0.97
Stem length (cm)	0.97	3.99*	1.13
No. ramets	21.9***	0.30	0.15
Shoot mass fraction (%)	0.35	0.77	0.09
Root mass fraction (%)	0.41	0.94	0.12

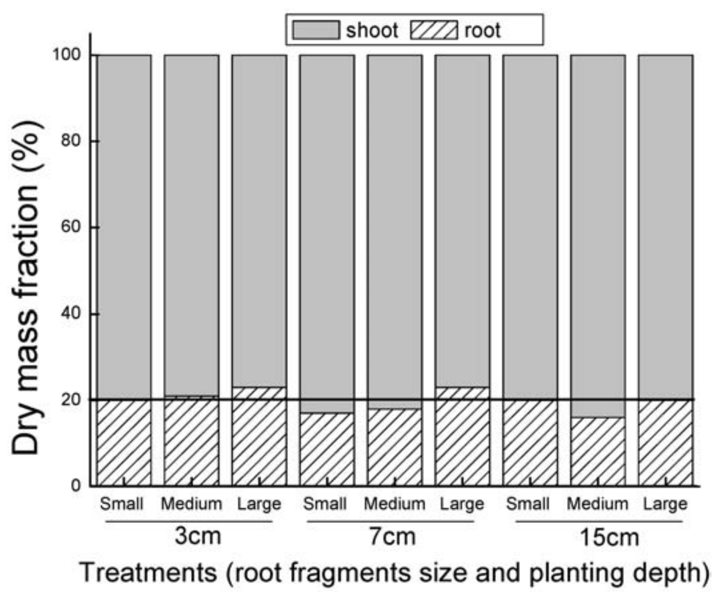

Figure 4. Effects of root fragment size and planting depth on biomass allocation of alligatorweed.

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