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REPORT

Phoenix clones: recovery after long-term defoliation-induced dormancy

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Abstract

Many long-lived plants are known to prolong dormancy in response to abiotic stresses such as drought. We are unaware, however, of any reports of plants prolonging dormancy in response to biotic stresses such as herbivory. We monitored 140 putative *Solidago missouriensis* clones (hereafter 'clones') ≥ 13 years before, during and after intense defoliation by the specialist herbivore *Trirhabda canadensis*. Eight of the clones produced no above-ground growth in the season following defoliation. Though apparently killed, these clones reappeared 1–10 years after they disappeared, with six of them robustly recovering in a single season. We used 38 RAPD markers to test the hypotheses (denoted by H and numbered with subscripts) that territories were recovered by (H_1) seedling establishment or (H_2) rhizomes. We compared pre-defoliation and post-recovery genotypes in two clones using the same 38 markers. Our data document the existence of very large clones (60–350 m^2 with c. 700–20 000 ramets), and support the hypothesis that recovery is from rhizomes. Within-clone diversity is low, and the pre-defoliation and post-recovery genotypes match. We consider mechanisms that could enable plants entering dormancy with depleted resources to robustly recover, and the implications of dormancy for avoiding biotic stress such as that induced by *T. canadensis*.

Keywords

Clone, defoliation, drought-induced dormancy, prolonged dormancy, RAPDs, *Solidago*.

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INTRODUCTION

A large fraction of plant species in temperate, boreal and alpine floras can propagate clonally, allowing genets (genetic individuals) to tolerate periods of reproductive failure, and often to attain great size and age (Jackson *et al.* 1985; Bond 1994; Steinger *et al.* 1996). However ramets (the independent shoots and their associated roots that comprise a genet) are genetically uniform, so the genet may be particularly vulnerable to extirpation by herbivores (Mopper & Strauss 1998), pathogens (Parker 1988; Schmid 1994; Wennstrom 1999) and other localized disturbance (Callaghan *et al.* 1992). In this paper we show that Missouri goldenrod (*Solidago missouriensis*) clones apparently killed through defoliation by the specialized beetle, *Trirhabda canadensis*, reappear two to many years later. In a single growing season these Phoenix clones reoccupy segments or the entirety of their original territories from rhizomes. The clones are as large as 350 m^2 with 20 000 ramets. We tested two hypotheses to explain the *en masse* reappearance of ramets in Phoenix clones. H_1: ramets are of recent seedling origin. H2: ramets are produced by rhizomes dormant since defoliation. A third hypothesis, reoccupation of the original territory via rhizomal spread from other clones or from occasional ramets that may have escaped defoliation, was rejected, because the number of rhizomes per ramet are too few and too short (Preus & Morrow 1999) to repopulate such large areas in a single growing season. We tested H_1 and H_2 using random amplified polymorphic DNA (RAPD) markers (Welsh & McClelland 1990). We predicted high within-clone genetic diversity among reappearing ramets if they were of seedling origin and low diversity if from rhizomes.

MATERIALS AND METHODS

Plant species

Goldenrods (*Solidago*, Asteraceae) constitute a widespread genus of over 100 species, most of which are native to North America (Zhang 1996). They are insect pollinated and

self-incompatible (Melville & Morton 1982) with small, wind-dispersed seeds that do not persist in the soil seed bank (Root 1996). Our study species, *Solidago missouriensis* Nutt. *var. fasciculata* Holz., is a rhizomatous herbaceous perennial of prairies and other dry, open or sparsely wooded places throughout central and western North America (Gleason & Cronquist 1991). Clones of *S. missouriensis* become established from seed in disturbed areas and are a persistent feature of mature grassland and savanna. Other plant species, primarily warm season grasses, co-occur in a clone's 'territory'. At our field sites, putative clones (spatially well defined groups of ramets, hereafter 'clones') are discrete, widely spaced (Morrow *et al.* 1989), and reach large size with thousands of ramets. In an Iowa prairie, *S. missouriensis* clones have been estimated to live 200–400 years with some reaching 1000 years (Whitham 1983).

Like its well-studied congeners *S. altissima* and *S. canadensis* (Abrahamson & Weis 1997), *S. missouriensis* has non-overlapping generations of ramets. In late summer, ramets initiate rhizomes before the above-ground stem dies in autumn; new ramets are produced from the apical tip of overwintering rhizomes in spring (Preus & Morrow 1999). Ramets are not produced at the same node in successive years, so genet survival depends upon annual production of ramets (Cain 1990). Whereas shoots are annual, *S. missouriensis* rhizomes can be more persistent with up to three generations being connected. Insect damage to shoots of *S. altissima* results in deterioration of rhizome connections, so that a given season's shoots and roots are physically independent from earlier generations (Maddox *et al.* 1989; How *et al.* 1994). With increasing insect damage to shoots of S. *missouriensis*, the number and length of rhizomes produced per ramet decreases from c. 2 rhizomes $\leq$ 20 cm long to $\leq$ 0.1 rhizome $<$0.5 cm long (Preus 1995; Preus & Morrow 1999).

Herbivore species

Goldenrods host many specialized phytophagous insects (Root & Cappuccino 1992; Root 1996). For *S. missouriensis*, the eruptive univoltine leaf beetle *Trirhabda canadensis* (Kirby) (Coleoptera: Chrysomelidae) has the greatest impact. Both larvae and adults feed on leaves from mid-May through July (Morrow *et al.* 1989). At our sites eruptions are confined to individual clones. More than other *Trirhabda* species, *T. canadensis* is very sedentary, dispersing from the natal clone only when all leaf tissue has been consumed. Before dispersing, females lay many eggs (Morrow *et al.* 1989).

Censuses

We monitored clones of *S. missouriensis* in a fire-maintained oak savanna remnant (Helen Allison Savanna (AS)) and in four fields abandoned from agriculture for more than 50 years in the adjacent Cedar Creek Natural History Area (CCNHA) in central Minnesota, U.S.A. (45°25′ N, 93°10′ W). Located on the Anoka sand plain, the soils are well drained, and low in organic matter and total nitrogen (Grigal *et al.* 1974). Locations and areas of clones on AS and one CCNHA field were mapped with a Leitz Total Station and SDR22 data logger. Locations of clones in the other three fields were mapped using metre tapes. An estimate of ramet density (10 random tosses of a 0.16-m^2 quadrat) was obtained when a clone was incorporated into the census. We annually monitored ramet densities and beetle eruptions, initially in 15 clones (1984) and by 1989, in 140 clones. Clones were permanently marked with stakes. Voucher specimens for the genotyped clones reported in this study are on deposit at the University of Minnesota Herbarium (MIN).

Clone fingerprinting

To test H_1 and H_2, we used RAPDs to characterize ramets that appeared in large numbers in territories previously occupied by defoliated clones and subsequently having no ramets. RAPD markers are especially useful for reconstructing within-species relationships; they are generally highly variable, can yield an essentially unlimited number of useful genetic markers per individual, and are relatively inexpensive to evaluate (Peakall *et al.* 1995).

Apices of ramets were field-collected, put on ice, returned to the laboratory and refrigerated or frozen until DNA extraction. DNA was extracted and analysed for RAPD markers using 15 ng DNA and five decamer DNA primers (OPF-03, 5′-CCTGATCACC-3′; OPF-04, 5′-GGTGATCAGG-3′; OPF-08, 5′-GGGATATCGG-3′; OPF-09, 5′-CCAAGCTTCC-3′; OPF-14, 5′-TGCTGCAGGT-3′; Operon Technologies, Alameda, CA) as in Olfelt *et al.* (1998), except that 0.1–0.2 g of apical meristem tissue was used, and RAPD markers were visualized through digital photography under UV light using a Kodak Digital Science DC 40 Camera and 1D image analysis software (Eastman Kodak Company, Rochester, NY). We extracted DNA independently from each of the ramets twice to confirm marker repeatability and DNA from all extractions was assayed in random order to avoid investigator bias in scoring. We scored each individual for the presence or absence of 38 markers, including only markers that gave consistent amplification in replicated extractions. Two ramets clone^{-1} from eight clones in different fields spread over the 2200 ha of CCNHA and AS were collected to estimate levels of RAPD marker variation in the *S. missouriensis* population.

We used Bayes' theorem,

$$P(B|A) = P(A|B)P(B)/P(A|B)P(B) + P(A|B^C)P(B^C)$$

(Grossman & Turner 1974) to estimate the probability that a ramet randomly selected from our entire sample of ramets would not be of the same genet [P(B)] when all 38 RAPD markers in the first ramet matched the pattern of the second ramet [P(A)]. Values for P(B) were estimated by dividing the number of ramets in each clone by the total number of ramets tested. The frequency of each marker state (present or absent) in our entire ramet sample was determined for each of the 38 markers in our study, and values of P(A) were then calculated for each clone using the product of that clone's 38 marker state frequencies.

In addition to the clones sampled to estimate marker variation, RAPDs were obtained from three groups of *S. missouriensis* clones. (1) In 1998 we tested our working assumption that a clone is a single genet by sampling 103 ramets along transects through clone AS-NE, which was about 500 m^2 with 17 000 ramets. Results of this sample (overwhelmingly one genotype) were used to determine an appropriate sampling intensity for Phoenix clones. (2) In 1999 we collected 5–11 ramets $clone^{-1}$ from six large clones whose defoliation, disappearance and reappearance we had documented. Ramets were sampled along a transect through each clone and were 2–10 m apart depending on clone size. (3) In 2001 we sampled ramets from a garden containing plots established with rhizomes obtained before clones AS-1 and AS-4 were defoliated and disappeared. Ramets from these plots provide pre-defoliation genotypes to compare with genotypes of ramets that subsequently appeared in the original territories of clones AS-1 and AS-4.

RESULTS

Of the 140 clones we monitored, 24 were completely defoliated by eruptions of *T. canadensis*. Most of these outbreaks were the result of introductions we made during experiments on beetle movement between 1989 and 1992. The natural frequency of outbreaks before 1985 and after 1998 was 0–2 $year^{-1}$. Many defoliated clones recovered entirely or in part after disappearing for ≥ 1 year, but some are still absent.

In clone AS-NE, 100 of the 103 ramets sampled had the same genotype. The probability of these ramets having identical RAPD genotypes (*P* identical but not of the same genet) is, conservatively, $< 2 \times 10^{-6}$). Three adjacent ramets in clone AS-NE shared a second genotype (*P* identical by chance $< 1 \times 10^{-7}$).

Each row in Fig. 1 shows the pre-defoliation size and history of a different Phoenix clone. The eight clones ranged in size from c. 60–350 m^2 with c. 700–20 000 ramets. All these clones failed to produce ramets the summer following defoliation. The entire pre-defoliation territories of clones 76-4 (Fig. 1a) and AS-58 (Fig. 1b) had ramets in the second and third year after disappearing, respectively. Reoccupation of clone AS-1's (Fig. 1c) territory occurred in three phases – a quarter densely filled with ramets 5 years after defoliation,

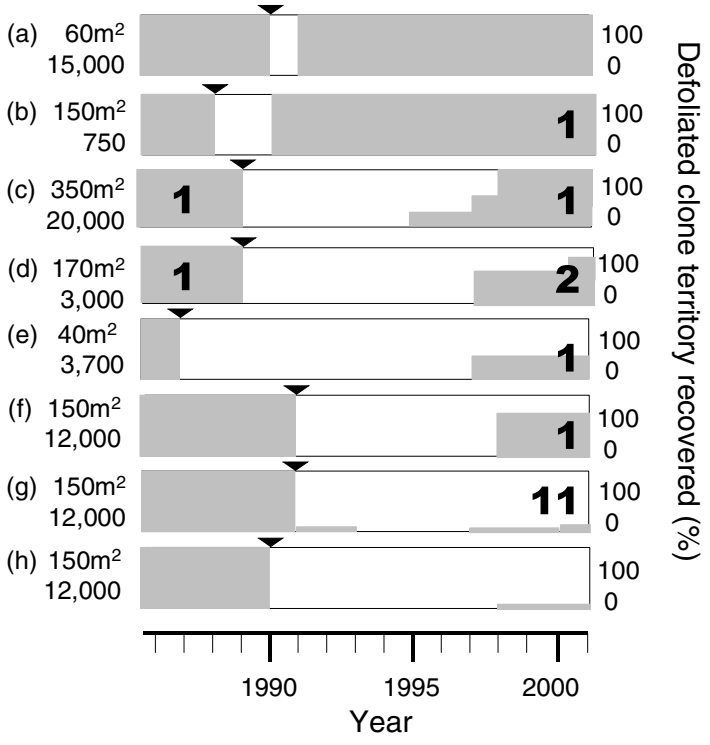

Figure 1 Characteristics and histories of eight *Solidago missouriensis* clones. Rows a–h represent clones 76-4, AS-58, AS-1, AS-4, AS-5, AS-6, AS-26 and 76-3, respectively. A clone's pre-defoliation area (m^2) and estimated number of ramets is given on the left. The centre panel shows a 15-year record of the presence and absence of ramets in each clone's territory. Absence of shading indicates an absence of ramets. ▼shows the beginning of dormancy, initiated by a *Trirhabda canadensis* eruption and defoliation. Reoccupation of entire or major segments of the original clone's territory by post-dormancy ramets is expressed as the percentage of the original clone's territory. The number of post-defoliation genotypes is shown at the right end of rows b–g. The numbers of genotypes present in common garden plots established with pre-defoliation ramets from AS-1 and AS-4 are given at the left end of rows c and d, respectively.

another quarter after 9 years, and the final half after 10 years. Clones AS-4 (Fig. 1d), AS-5 (Fig. 1e) and AS-6 (Fig. 1f) have so far densely recovered only portions of their original territories. Clones AS-26 (Fig. 1g) and 76-3 (Fig. 1h) had, respectively, just 11 and 10 small, well-separated clusters of ramets that appeared 7 and 9 years, respectively, after defoliation, and occupied less than 10% of the original territory. The number of years different genets remained dormant varied, but there was little variation in the time of recovery among physiologically disconnected rhizomes of the same genet.

The number of post-defoliation genotypes present in six of the eight Phoenix clones is shown on the right side of each row in Fig. 1. None of the clones shared genotypes. AS-58, AS-1, AS-6 and AS-5 (Fig 1b,c,e,f, respectively) each had a single genotype; AS-4 (Fig. 1d) had two genotypes (seven ramets of one, one of the second). The probability that post-defoliation ramets in the same pre-defoliation clone territory were identical by chance yet not the same genet is remote ($< 1 \times 10^{-14}$).

For the two clones for which we had pre-defoliation ramets, the genotype of AS-1 (Fig. 1c) was the same as its Phoenix clone. The Phoenix clone AS-4 (Fig. 1d) had two genotypes, one of which was prevalent: this common genotype matched the pre-defoliation genotype found in the common garden.

In contrast to the other Phoenix clones, all 11 ramets sampled in clone AS-26 (Fig. 1g) had different genotypes.

DISCUSSION

The very low genetic diversity of ramets sampled from clone AS-NE is consistent with our working assumption that seedling establishment is a rare event (Hartnett & Bazzaz 1985; Cain 1990) and that clones are generally one or a few genets. The low genetic diversity in post-recovery clones AS-1, AS-4, AS-5, AS-6, and AS-58 supports hypothesis 2: ramets appearing in a defoliated clone's territory are produced by long-dormant rhizomes of the pre-defoliation clone. This hypothesis is further supported by the match between genotypes of ramets growing in plots established with pre-defoliation rhizomes from clones AS-1 and AS-4 and post-recovery ramets from the same territories (Fig. 1).

Our data are not consistent with the hypothesis that ramets appearing in a defoliated clone's territory originated from seedlings established after the original clone disappeared (H_1). The seedling hypothesis would require high genetic diversity among the ramets, because goldenrods are self-incompatible and because large numbers of seedlings would be needed to reoccupy an area that is enormous relative to the area a seedling could occupy in 1 year. Clone AS-26 might be an exception since all of the ramets sampled in it were different, showing that it is an assemblage of many genets. However, there is evidence that AS-26 is located in a site that was a horse corral before the 1930s (Chapman & Faber-Langendoen 1991). Thus soils would have been repeatedly disturbed, allowing for multiple episodes of seedling establishment. Ramets reappearing after AS-26 was defoliated in 1990 are most likely produced by rhizomes of the pre-defoliation genets. If the ramets were from post-defoliation seedlings, seed would have to have dispersed into the AS-26 territory from a non-dormant clone and would have been as likely to land and germinate outside as inside the pre-defoliation territory. No *S. missouriensis* ramets have been found beyond AS-26's mapped territory. Moreover, this area has not been disturbed since defoliation, so few safe sites were available for seedling establishment.

The most commonly reported incidents of prolonged dormancy occur in dry or seasonally dry habitats and for species with prominent storage organs such as corms, bulbs and tubers (Hoffman & Parsons 1993). Entire populations of seven tuberous perennials (*Delphinium* spp., Ranunculaceae) prolonged dormancy up to 9 years in response to especially dry summers (Epling & Lewis 1952). Apparently in response to late arrival of winter rains in the Negev Desert, between 10 and 70% of adult wild tulips failed to emerge for $\leq$ 4 years (Boeken 1991). Vaughton & Ramsey (2001) demonstrated a genetic basis for prolonged dormancy in populations of the lilioid geophyte *Burchardia umbellata* at sites with different probabilities of experiencing extended drought.

Prolonged dormancy may be much more common than is presently appreciated if it also occurs in species that do not have such prominent storage organs. We found only one study documenting drought-initiated disappearance of non-geophytes. Throughout a severe 7-year drought, 21 prairie species in the Asteraceae (including *S. missouriensis*), Boraginaceae, Fabaceae, and Poaceae were rare or absent from permanent plots. When rains returned, these species were the first to reappear, presumably recovering from 'long dormant' rhizomes and crowns (Albertson & Weaver 1944; Weaver 1968). In response to habitat-wide drought, these plants escape water stress by prolonging dormancy. The benefit is clear, and the signal for recovery is adequate moisture (Albertson & Weaver 1944; Weaver 1968).

Prolonged dormancy also occurs in mesic habitats. Some individuals of the orchid *Cypripedium calceolus* may become dormant for up to 4 years in swampy areas studied by Shefferson *et al.* (2001), and Hutchings *et al.* (1998) estimated that most individuals in several populations of the English orchid *Orchis militaris* extended annual dormancy at least once in every 3 years. In a study of marked individuals of swamp milkweed, Breaden (1999) noted that individuals had disappeared for up to 2 years. The reasons individuals prolong dormancy in these species are unknown.

In *S. missouriensi*s, the synchronous disappearance (and later reappearance) of defoliated clones suggests that clones enter prolonged dormancy in response to recurring, severe damage by erupting populations of host-specific beetles. Unlike the species entering dormancy in the mesic systems cited above, our prairie sites experienced drought, including a 3 year period during our censuses (1987–89). This drought did not result in dormancy in the *S. missouriensis* population. The factor signalling the breaking of dormancy among the physically disconnected rhizomes of a dormant genet is not known. However, a strong abiotic signal, breaking of the drought, did not result in simultaneous recovery of the different Phoenix clones (Fig. 1); clones recovered in dry, normal and wet years.

A lengthy period of dormancy should have biotic consequences for a *S. missouriensis* clone. A benefit of disappearance is that the clone escapes resident herbivores. Before immigrating from a defoliated clone, *T. canadensis* females lay many eggs in the clone's territory. Larvae emerging the following spring feed on emerging ramets, extending the outbreak another year. If the clone is dormant one year, larvae starve and the outbreak is, within this clone, over. By being absent in additional years, Phoenix clones escape being recolonized if beetles in neighbouring clones later erupt and disperse (Morrow, P. A. & Puttick, G., unpublished data). Populations of *Eurosta comma,* a *S. missouriensis*-specific rhizome galler, are also extirpated when a clone prolongs dormancy. Typically 10–25% of a clone's ramets are galled. After Phoenix clones reappear, *Eurosta* recolonization takes several years. The proportion of ramets galled was significantly lower in Phoenix clones that had reappeared in the previous two to three years than in clones which had been active above-ground for at least 7 years (Preus 1995).

A potential disadvantage of entering dormancy is that co-occurring grasses and forbs sharing the clone's territory should benefit from the absence of a competitor. If neighbours did benefit, however, it did not prevent robust recovery of Phoenix clones.

Unlike instances of extended seasonal or drought dormancy, Phoenix clones disappear during the growing season after defoliation has greatly depleted above- and below-ground resources (Preus & Morrow 1999). How do dormant rhizomes obtain or sequester the resources to robustly recover years later? One possibility is that defoliation may reverse the early growing season pattern of allocating stored resources to new shoots. Instead these resources may be sequestered in the ramet's crown or rhizome to provision dormant buds and fuel later recovery. Changes in allocation could be triggered by a loss of apical dominance and decrease in sink strength in defoliated shoots (Honkanen & Haukioja 1998) or could be a genetically based, induced response (Karban & Baldwin 1997; Strauss & Agrawal 1999; Hochwender *et al.* 2000). The latter is suggested by the timing of clone recovery, which varies among (Fig. 1), but is relatively uniform within the whole or large segments of a genet's territory.

The orchid *Cypripedium acaule* also enters dormancy with depleted resources (a consequence of flowering) for a recovery period lasting 2–3 years on average (Primack & Stacy 1998). Orchids may acquire resources for their recovery via their mycorrhizal associates (Smith & Read 1997). The possibility exists that Phoenix *S. missouriensis* clones obtain resources from neighbouring plants via shared arbuscular mycorrhizae (AM). *S. missouriensis* is extensively colonized by AM fungi (P. Avis, unpublished data) and strongly mycorrhizal plants (e.g. *Andropogon gerardii*) grow within clones' territories. Two recent reports make this suggestion even more plausible. Bidartondo *et al.* (2002) report that three non-photosynthetic plant species associate with AM fungi, suggesting that these fungi can deliver as well as receive carbon. Presumably the non-photosynthetic plants obtain fixed carbon from mycorrhizal networks linked to green plants. In a field experiment, Lerat *et al.* (2002) showed that ^{14}C moved between two species linked by AM. Sugar maple seedlings received carbon from a spring ephemeral (*Erythronium*) as the maple began to leaf out. Later, the *Erythronium* obtained carbon from the leafed out maple when it was initiating an autumn set of leaves and roots.

Prolonged dormancy could explain how clones of *S. missouriensis* and probably other clonal species are able to persist for hundreds of years (Whitham 1983) in biotically and abiotically variable environments. The unexplained prolonged dormancy of individuals of other species might have biotic triggers, and could be much more widespread than appreciated. As pointed out by Lesica & Steele (1994), being unaware of the extent of prolonged dormancy may result in underestimates of plant population densities, especially in endangered geophyte species, and in overestimates of plant mortality in demographic studies.

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