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Seed Dispersal and the Spread of Weeds

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Abstract

Weeds colonize new habitats and maintain genetic variation between existing populations by seed dispersal. I briefly discuss current evolutionary theories regarding the selection pressures acting on plants to disperse their seeds, and how they are relevant to herbaceous weeds. Many weed seeds disperse by wind or by adhering to animal fur or feathers (burrs). Wind-dispersed seeds from low-growing weeds often do not travel long distances, mainly because their low height of release does not allow them to be airborne for long periods of time. By contrast, burrs can adhere to and be carried by their dispersal agents indefinitely, and so have the potential to travel very long distances. More herbaceous weed species are wind-dispersed than burr-dispersed despite the longer dispersal distance achieved by burrs. I suggest that this is because wind is a more reliable dispersal agent in the relatively open habitats where herbaceous weeds occur.

La Dispersion des Graines et la Propagation des Mauvaises Herbes

C'est au moyen de dispersion de graines que les mauvaises herbes colonisent des habitats nouveaux et qu'ells maintiennent la variation génétique entre leurs populations actuelles. Je passe en revue brièvement les théories d'évolution admises à propos des pressions sélectionelles qui amènent des herbes à disperser leurs graines, ainsi que la manière dont ces thérories s'appliquent aux mauvaises herbes. Beaucoup de graines de mauvaises herbes se dispersent au moyen du vent ou en s'attachant au pelage ou aux plumes d'animaux. Fréquemment, les graines de mauvaises herbes ne traversent que des distances courtes, parce que la petite hauteur à laquelle elles sont lâchées ne leur permet pas de se faire transportés longtemps par le vent. Par contre, les capsules épineuses, qui peuvent s'attacher indéfiniment aux agents de dispersion, ont le pouvoir de traverser de longues distances. Plus d'espèces de mauvaises herbes doivent leur dispersion au vent, qu'aux capsules épineuses, malgré la superiorité de celles-ci comme voyageurs. Je considère qu cela resulte de la plus grande sûreté du vent comme agent de dispersion dans les habitats relativement ouverts, où se trouvent les mauvaises herbes.

Introduction

Seed dispersal is the means by which plants colonize new habitats: the spread of weeds is contingent on widespread seed dispersal and the ability of seedlings to establish and reproduce in a variety of environmental conditions (Salisbury 1961). (For convenience, all plant propagules will be referred to as 'seeds', even though they may technically be achenes, nutlets, etc.) The influx and establishment of seeds into new habitats has consequences for weed control. Firstly, seed dispersal may promote the introduction of exotic species into geographic regions where their limiting agents do not exist (Room 1981). In addition, seed dispersal promotes gene flow and introduces and maintains genetic variation between and within plant populations. This is relevant to weed control because asexual, uniform populations are thought to be easier to control than genetically diverse populations (Burdon *et al.* 1981). Likewise, the input of small numbers of seeds ('founder populations') into new habitats may result in populations with low genetic variation (especially if plants reproduce asexually) and these may be somewhat easier to control (Harper 1977).

The evolutionary factors selecting for dispersal of seeds away from the parent plant are discussed in detail in Howe and Smallwood (1982). Three selection factors have been hypothesized as acting on seed dispersal: (1) escape from the parent plant; (2) colonization of new habitats; and (3) 'directed', or non-random dispersal of seeds to favorable habitats.

These hypotheses are not mutually exclusive. The first two hypotheses concern dispersal distance. The 'escape' hypothesis postulates that mortality due to seed predation, fungal pathogens, and sibling competition is greater below the parent plant than anywhere else, so that long-distance dispersal away from the parent plant is favored (Augsberger 1983). This hypothesis generally applies to plants growing in stable habitats. The 'colonization' hypothesis applies to plants occupying the early stages of succession. These early colonizers produce an environment where other plant species become competitively superior, and the original plants are then under strong selection pressure to disperse seeds to new, unoccupied habitats (Horn 1974). 'Directed' dispersal concerns plants occupying habitats with special edaphic conditions, so that non-random dispersal to habitats with the same conditions is more important to fitness than dispersal distance. 'Directed' dispersal is probably not relevant to weeds, which are characterized by their wide tolerance of environmental conditions.

A fourth type of dispersal that is common in weedy plants is dispersal through 'time'. Seeds that disperse through time do not possess morphological adaptations for long distance dispersal (pappus, barbs, fleshy fruits), but are viable in the soil for long periods of time (50 years is not uncommon; Werner 1979). The habitats occupied by species that disperse through time are usually inhospitable to prolonged adult survival, often because they are continually disturbed (Werner 1979). 'Dispersal' occurs when seeds germinate and establish in the sites previously occupied by their parents.

This paper deals principally with long-distance dispersal since it is the means by which weeds spread and colonize new habitats. First, I review the major mechanisms by which seeds of herbaceous weedy plants disperse away from the parent plant. Second, I discuss differences in the dispersal distance achieved by wind and adhesively dispersed seeds. I briefly describe some experimental results showing how the morphological characteristics of burrs influence dispersal distance. Finally, I put forward some hypotheses to explain why selection has favored wind over adhesive dispersal in many weed species. The mechanisms discussed (and arguments developed) in this paper are restricted to terrestrial weeds of short (1.5 m or less) stature.

Seed Dispersal Mechanisms of Weeds

Weeds are often spread to new continents by human activities (Salisbury 1961; J.H. Myers, pers. comm.). Most herbaceous weed seeds that disperse to new habitats are transported by wind (308/544 species of 'weedy' Compositae) and adhesively on animal fur or feathers (57/544 species of 'weedy' Compositae). (The remainder of the 544 species are dispersed through 'time' or using scales that function in orientation during dispersal and on the ground; data from a pan-global survey of 18 regional floras by Venable and Levin (1983). See Werner (1979), and Howe and Smallwood (1982) for data on dispersal mechanisms of other plant families.) Relatively few herbaceous plants disperse their seeds as fleshy fruits; this dispersal mode is mostly restricted to woody plants (Levin and Kerster 1974; Sorensen 1981, 1984). Seeds that possess morphological adaptations for long-distance dispersal do not usually remain viable in the soil for long periods of time, and many plants which produce seeds with morphological adaptations for dispersal are also able to reproduce vegetatively by cloning (Werner 1979; Venable and Lawlor 1983). It has been hypothesized that dispersal is at a premium in perennials because there are few sites for recruitment near the parent plant (Cook 1979; Werner 1979).

The distance travelled by wind-dispersed seeds is principally determined by the height of seed release, the speed that the seed falls through the air (terminal velocity), the speed and turbulence of the wind between the ground and the point of release, and the presence of obstructions in the seed's path (Harper 1977). Wind-dispersed seeds from plants of short stature (i.e. herbaceous weeds) growing in dense stands usually travel short distances because of their low height of release and the presence of obstructions (Harper 1977). Even when obstructions are not present (i.e. the habitat is not densely vegetated), the distance travelled by wind-dispersed seeds of short herbaceous plants is often not more than a few metres (Harper 1977; Waser *et al.* 1982; but see Platt 1975 for examples of wind-borne seeds that can travel several hundred metres).

Adhesively dispersed seeds (burrs) have the potential to be transported much longer distances than wind-dispersed seeds because they can be carried indefinitely on animal fur or feathers. Adhesive seeds may remain on animals until the animal molts or dies (Agnew and Flux 1970). Burrs may travel shorter distances if they passively drop off, or they are detected and removed by the animal shortly after attachment. However, even a short retention time may result in relatively long-distance dispersal if the host animal travels at a good speed.

Burr Morphology and Dispersal Distance

The potential for long distance seed dispersal may make the spread of burr-bearing weeds particularly difficult to control. The pan-global occurrence of several species of economically important weeds must be attributed, at least in part, to long distance seed dispersal of their burrs. Three cosmopolitan weeds, *Xanthium* spp. (Compositae; cocklebur, noogoora burr), *Arctium* spp. (Compositae; burdock), and *Tribulus* spp. (Zygophyllaceae; puncture vine) are dispersed as burrs. The burrs of *Xanthium* and *Arctium* seriously decrease the value of wool (Gross *et al.* 1980; Weaver and Lechowicz 1982), and *Tribulus* burrs cause stress to livestock and may puncture the stomach linings of the animals that consume them (Sankaran and Ramaseshiah 1981). In addition, forage of *Arctium* and *Tribulus* is poisonous to livestock and all three species compete with crop plants (Gross *et al.* 1980; Sankaran and Ramseshiah 1981).

The burr morphology of *Arctium* spp. and *Xanthium* spp. varies greatly within species, populations, and individual plants (Hawthorn and Hayne 1978; Hare and Futuyma 1978). I hypothesize that this variation in burr size and morphology has an important influence on seed dispersal distance. I predict that burrs of certain sizes and shapes are very irritating to animals, and that these burrs will be removed shortly after attachment. I tested the following hypotheses using burdock (*A. minus* [Mill.] Bernh.) burrs and captive snowshoe hares (*Lepus americanus* Erxleben) (Lagomorpha: Leporidae): (1) Small burrs are less irritating to animals than large burrs, and so should be retained for longer periods of time than large burrs; (2) Burrs attached to the pads of animal's feet are more noticeable than burrs attached to other body areas (e.g. the back). Back burrs should therefore be retained longer (and travel farther) than feet burrs; and (3) Burrs attached to an animal in low numbers (e.g. 2 burrs/hare) are less irritating to animals than burrs attached in high numbers (e.g. 16 burrs/hare), and so should be removed less quickly. That is, the mean retention time of a burr should be longer for burrs attached in low numbers than burrs attached in high numbers.

From the plant's perspective, the first hypothesis refers to whether selection for long-distance dispersal has favored the production of burrs of a certain size. The second hypothesis refers to whether a plant drops its burrs to the ground (where they would attach to an animal's feet), and the height of burrs in relation to where they attach to an animal. The third hypothesis refers to the numbers of burrs that detach from the plant during an encounter with an animal.

The experiment testing these hypotheses involved applying *A. minus* burrs of different sizes and numbers to different body positions of four captive snowshoe hares. The experimental results confirmed all three hypotheses: (1) small burrs were retained longer than large burrs; (2) burrs on the back were retained longer than burrs on the feet; and (3) burrs attached to hares in low numbers had longer mean retention times than burrs attached in high numbers. All these results were statistically significant (Sorensen, in prep.). Moreover, it was not uncommon for the burrs to be retained for up to 24 h, which could result in dispersal to long distances. The relationship between burr characteristics, retention time, and dispersal distance in the field will also be determined by the distance travelled by the animal in its home range, and whether burrs are knocked off the animal by chance.

The relationship between burr size, burr number, dispersal agent body position ('feet' *vs.* 'back') and retention time has implications for the evolution of burr and plant characteristics. Since burr size and seed number are positively correlated in *A. minus* (burr weight and seed no., $r = .839$, $N = 50$; burr length + width and seed no., $r = .768$, $N = 50$), small burrs may go longer distances than large burrs, but fewer seeds are dispersed/burr. Likewise, burrs attached in low numbers may be retained on animals for long periods of time, but fewer seeds are dispersed than when burrs are attached in high numbers. Finally, with regard to the longer retention time of 'back' burrs compared to 'feet' burrs, it may be relevant that *A. minus* plants drop relatively few of their burrs to the ground (approximately 20% dropped, Hawthorn and Hayne 1978). Another species of *Arctium*, *A. lappa*, drops up to 60% of its burrs (Hawthorn and Hayne 1978). Many of the 'dropped' *A. lappa* burrs may be taken to new locations by the wind, but some must stick to the feet of animals. *A. lappa* plants probably disperse more burrs than *A. minus* plants (which may have low burr removal rates; Hawthorn and Hayne 1978), but the *A. minus* burrs that do attach to dispersal agents may travel longer distances. Future research will test these generalizations by examining the distance travelled by marked burrs.

Adhesive *vs.* Wind Dispersal

I have argued that many weedy plant species are under strong selection pressure to disperse their seeds to new habitats. I have also argued that adhesive seeds have the potential to disperse to much greater distances than wind-dispersed seeds. These arguments appear to contradict the evidence: in general more 'weedy' plant species are dispersed by wind than by adhesion (Werner 1979; Venable and Levin 1983). I hypothesize that there is strong selection against adhesively dispersed seeds because their encounter rates with dispersal agents may often be low. For example, there is evidence that individual plants of *A. minus* and *Daucus carota* L. (Umbelliferae) have very few of their burrs removed by animals (Hawthorne and Hayne 1978; Lacey 1981) during a season. Selection may favor wind-dispersal in habitats where plants are under strong selection pressure to disperse seeds away from the parental site because wind is a more reliable (albeit less effective) dispersal agent. By contrast, most of the relatively open (disturbed and cultivated) habitats where weeds occur almost always receive some wind, but visits by animals may be infrequent. (Burrs may be more common than wind-dispersed seeds in closed habitats which receive almost no wind, such as the forest floor; Stebbins 1974.) Future work will involve testing these hypotheses by examining the removal rates and distances travelled by wind and adhesively dispersed seeds in the field.

Some weed species exploit both wind and adhesive dispersal agents by producing heteromorphic seeds. Two composite species (*Picris echioides* L. and *Hypochoeris glabra* L.) produce dimorphic seeds where one morph is wind-dispersed and the other morph is adhesively dispersed (Sorensen 1978; Baker and O'Dowd 1982). In both species, the adhesively dispersed seeds occur on the periphery of the capitulum and are slightly larger than the wind-dispersed seeds. The morphs do not differ in germination or competitive ability, and the main difference between them appears to be dispersal. The ratio of animal to wind-dispersed seeds of *H. glabra* varies according to plant density: high ratios of adhesive to wind-dispersed fruits are produced when plants grow in dense stands. This is thought to be advantageous to *H. glabra* plants because obstructions by neighbouring plants reduce the efficiency of wind-dispersal (Baker and O'Dowd 1982). The production of heteromorphic seeds ensures transport away from the parent plant even if only one dispersal agent is available. In addition, successful seed transport by both agents promotes the dispersal of seeds to a variety of distances and habitats. The spread of *P. echioides* and *H. glabra* may be limited only by the ability of seeds to establish and reproduce in the sites where they land.

Conclusions

Seed dispersal is responsible for the spread of weeds into new habitats and also for maintaining genetic variation within pre-existing weed populations. Both these factors have implications for weed control.

Many weed seeds are dispersed away from the parent plant by wind or by adhesion to animal fur or feathers (burrs). Burrs have the potential to travel farther than wind-dispersed seeds because they can be carried on animals for very long periods of time. Experimental results suggest that the morphological characteristics of burrs affect how long they remain on an animal before they are groomed off. This finding has implications for the evolution of plant characteristics, and may provide important clues on how weeds spread.

Despite the potential of burrs to disperse to proportionately longer distances, more species of weedy plants are dispersed by wind. I hypothesize that this is because wind is a more reliable dispersal agent in the open, disturbed areas where weeds occur. This hypothesis needs to be tested by monitoring seed removal rates of weeds producing wind- and adhesively-dispersed seeds in a range of habitats. The relationship between plant characteristics, seed dispersal, and the spread of weeds clearly deserves further work.

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