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Reversal of height dimorphism promotes pollen and seed dispersal in a wind-pollinated dioecious plant

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Variation in the timing of reproductive functions in dioecious organisms may result in adaptive changes in the direction of sexual dimorphism during the breeding season. For plants in which both pollen and seeds are wind-dispersed, it may be advantageous for male plants to be taller when pollen is dispersed and female plants to be taller when seeds are dispersed. We examined the dynamics of height dimorphism in *Rumex hastatulus*, an annual, wind-pollinated, dioecious plant from the southern USA. A field survey of seven populations indicated that females were significantly taller than males at seed maturity. However, a glasshouse experiment revealed a more complex pattern of height growth during the life cycle. No dimorphism was evident prior to reproduction for six of seven populations, but at flowering, males were significantly taller than females in all populations. This pattern was reversed at reproductive maturity, consistent with field observations. Males flowered later than females and the degree of height dimorphism was greater in populations with a later onset of male flowering. We discuss the potential adaptive significance of temporal changes in height dimorphism for pollen and seed dispersal, and how this may be optimized for the contrasting reproductive functions of the sexes.

Keywords: dispersal; phenology; plant height; sexual dimorphism; wind pollination

1. INTRODUCTION

Reproductive success in outcrossing plants depends on the effective dispersal of pollen and seeds. For species with separate sexes (dioecy), selection on the contrasting reproductive functions of females and males can result in sexual dimorphism in morphological and phenological traits [1]. Pollen- and seed-dispersal vectors (animals, water or wind) used by species will also influence selection on the sexes. In wind-pollinated (anemophilous) species, plant height plays an important role in promoting pollen dispersal because of the aerodynamics of pollination. It is generally advantageous for the male reproductive organs to be positioned above (or at least equal to) the female organs [2], and greater pollen dispersal and increased mating opportunities are expected for taller plants [3]. Similarly, for

species that rely on wind for seed dispersal (e.g. winged seeds), seed-release height is an important determinant of dispersal distance [4]. Greater seed dispersal is associated with a number of benefits, including reduced sibling competition [5] and colonization of favourable sites [6]. Sexual height dimorphism in wind-pollinated species may therefore be expected to vary across the life cycle, according to the contrasting timing of pollen- and seed-dispersal functions.

Here, we examine the temporal dynamics of height dimorphism in *Rumex hastatulus*, a wind-pollinated dioecious plant. We predicted that males should be taller than females at flowering, but that this pattern might be reversed at seed maturity owing to the benefits of improved seed dispersal. We examined these predictions by surveying plant height in natural populations, and conducted a glasshouse experiment under uniform conditions in which we investigated height change throughout the life cycle. We also considered the extent to which differences between the sexes in the phenology of flowering might influence height dimorphism.

2. MATERIAL AND METHODS

Rumex hastatulus (Polygonaceae) is a colonizer of fields and open, disturbed ground and is distributed across the southern regions of the USA from Texas to North Carolina and Florida. It is cytologically complex with two distinct chromosome races: the North Carolina karyotype and the Texas karyotype [7]. Plants are winter annuals (or less often short-lived perennials) overwintering as a basal rosette until spring when they usually produce several inflorescences. The species has winged fruit and seed are wind-dispersed.

During April–May 2009, we measured female and male height at reproductive maturity (seed maturation for females) in seven populations across the geographical range (table 1). In each population, we randomly sampled 51–63 females and males along a transect ($n = 425$ females and 393 males). We measured height from the soil surface to the tip of the longest stem. For each population (and for FL-MAR; table 1), we collected open-pollinated seed families. In September 2009, we germinated 36 seeds from each population from three randomly chosen families in Petri dishes on moist filter paper in a growth cabinet maintained at 20°C for 12 h and 10°C for 12 h with continuous light. After approximately 14 days, we transplanted 21–36 seedlings per population individually to 5 cm pots containing Pro-Mix BX (peat moss, vermiculate and perlite) and NPK fertilizer (20 : 20 : 20) and these were grown in a glasshouse at 20–24°C. The 261 seedlings were positioned in a complete randomized block design.

At three stages: (i) pre-reproduction (four weeks), (ii) date of first flowering, and (iii) reproductive maturity (eight weeks), we measured height from the pot surface to the tallest point on the plant (basal rosette leaf height or flowering stem). At first flowering, we recorded the date and sex of each plant and calculated days to first flowering.

We examined the effect of population and sex on height at seed maturity for the seven populations using REML linear-mixed models. Similarly, for our glasshouse experiment, we used REML linear-mixed models to examine if: (model 1) sexual dimorphism for height varied among reproductive stages and populations; and (model 2) days to first flowering varied among populations and between sexes. For both models, population and sex were fixed factors, and we added reproductive stage to the first model. Block and family (nested within population) were added to the random model, as was sampling time for the first model. We used the least significant difference (at $\alpha = 0.05$) to examine differences among groups, and linear regression to examine the relation between the degree of dimorphism in days to first flowering and height at first flowering. For all analyses, we used GENSTAT for WINDOWS 13th edition (VSN International, Oxford, UK).

3. RESULTS

In all populations of *R. hastatulus*, female plants were significantly taller than males at reproductive maturity (figure 1a and table 2). However, when populations were grown under uniform conditions in the glasshouse a more dynamic picture emerged involving

Table 1. Mean field and glasshouse height (at reproductive maturity) and mean days to first flowering in eight populations of *Rumex hastatulus*. State codes: FL, Florida; NC, North Carolina; TX, Texas.

race	pop code	latitude	longitude	field height (mm) (mean \pm s.e.)		glasshouse height (mm) (mean \pm s.e.)		days to first flowering (mean \pm s.e.)	
				female	male	female	male	female	male
NC	FL-CHI	29° 31' 44" N	82° 53' 4" W	400.5 \pm 11.9	347.9 \pm 12.8	717.5 \pm 32.2	663.3 \pm 28.5	45.2 \pm 2.1	47.6 \pm 1.8
NC	FL-MAR	30° 48' 43" N	85° 11' 28" W	474.3 \pm 11.9	358.1 \pm 12.3	760.6 \pm 23.0	624.3 \pm 22.9	40.9 \pm 1.5	46.9 \pm 1.5
NC	NC-BAT	36° 6' 59" N	77° 48' 35" W	532.3 \pm 12.2	441.5 \pm 12.6	673.1 \pm 38.6	642.1 \pm 38.3	44.7 \pm 2.5	51.4 \pm 2.4
TX	NC-HIC	35° 31' 32" N	76° 52' 18" W	362.0 \pm 11.9	299.2 \pm 12.1	719.7 \pm 19.0	655.0 \pm 19.5	40.9 \pm 1.2	41.0 \pm 1.2
TX	TX-ATH	32° 11' 5" N	95° 48' 12" W	364.8 \pm 12.4	313.5 \pm 13.3	730.7 \pm 28.4	658.2 \pm 26.1	40.6 \pm 1.8	41.9 \pm 1.7
TX	TX-KEN	31° 19' 31" N	95° 22' 12" W	380.7 \pm 12.7	321.1 \pm 13.3	701.6 \pm 21.9	561.6 \pm 23.5	40.0 \pm 1.4	42.5 \pm 1.5
TX	TX-OAK	31° 33' 39" N	95° 54' 6" W	313.5 \pm 12.7	264.0 \pm 12.6	710.1 \pm 20.3	658.9 \pm 20.0	39.4 \pm 1.3	43.2 \pm 1.3
TX	TX-ROS	31° 7' 3" N	96° 51' 37" W						

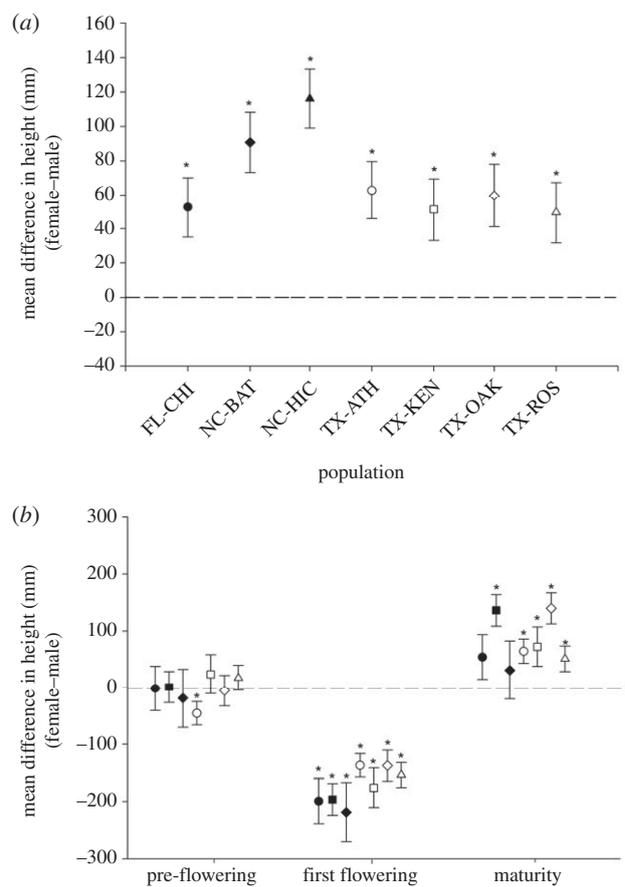


Figure 1. Mean difference in height (female–male) of *Rumex hastatulus* plants for (a) seven field populations at reproductive maturity and (b) seven populations at three reproductive stages in the glasshouse. For (b), pre-flowering is after four weeks' growth, first flowering is the onset of flowering and reproductive maturity at seed maturation (eight weeks' growth). The dashed line represents no difference in height of females and males. Values above the line indicate that females are taller than males and below the line that males are taller than females. Filled circles, FL-CHI; filled squares, FL-MAR; filled diamonds, NC-BAT; open circles, TX-ATH; open squares, TX-KEN; open diamonds, TX-OAK; open triangles, TX-ROS. Filled symbols represent the North Carolina race and open symbols the Texas race. Asterisks (*) represent significant difference in height from the least significant difference at $\alpha = 0.05$.

temporal changes in height during the life cycle. The degree and direction of sexual dimorphism for plant height varied among populations and at each reproductive stage (figure 1b and table 2; population \times sex \times reproductive stage, $p = 0.045$). Prior to reproduction (four weeks), there was no significant difference in height between females and males for six of the seven populations (figure 1b); in one population (TX-ATH), males were significantly taller than females. In contrast, at first flowering, males were significantly taller than females in all populations (figure 1b). This pattern reversed at seed maturity (eight weeks) in five of seven populations with females significantly taller than males (figure 1b).

We detected significant sexual dimorphism in the timing of first flowering among all populations (table 2; population \times sex, $p > 0.05$). In males, onset of flowering was significantly later than females (table 1,

Table 2. REML analyses examining the effect of (a) population and sex (female or male) on height at reproductive maturity in seven field populations of *Rumex hastatulus*, (b) population, sex and reproductive stage on height and (c) population and sex on days to first flowering for seven populations grown in the glasshouse. Significant p values ($\alpha = 0.05$) are indicated in bold.

	d.f.	F	p
(a) height in the field			
population	6	55.51	<0.001
sex	1	109.53	<0.001
population \times sex	6	2.10	0.051
(b) height in the glasshouse			
population	6	2.55	0.065
sex	1	16.12	<0.001
reproductive stage	2	3271.80	<0.001
population \times sex	6	0.88	0.512
population \times reproductive stage	12	5.93	<0.001
sex \times reproductive stage	2	165.02	<0.001
population \times sex \times reproductive stage	12	1.81	0.045
(c) days to first flowering			
population	6	4.54	0.011
sex	1	15.82	<0.001
population \times sex	6	1.64	0.139

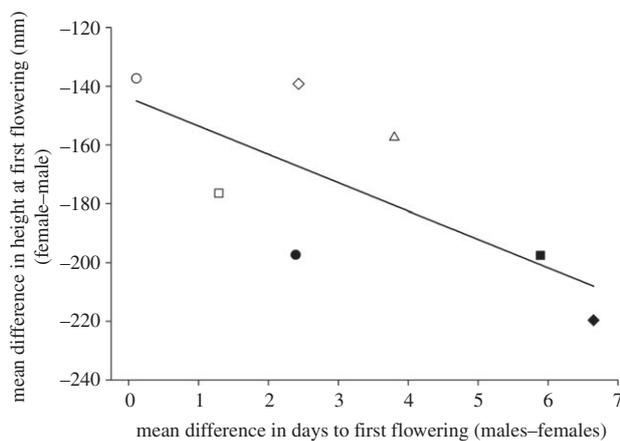


Figure 2. The relation between sexual dimorphism in days to first flower and height at first flower for seven populations of *Rumex hastatulus* ($r^2 = 0.43$, $p = 0.065$). The equation for this relation is $y = -9.74x - 143.6$. For population symbols, see figure 1.

$p < 0.001$) with the mean difference between sexes ranging from 0.1 to 6.7 days among populations. There was a marginally significant relation between the difference in days to first flower between sexes and the degree of height dimorphism at first flowering ($r^2 = 0.43$, $p = 0.065$; figure 2). Populations in which males flowered later than females exhibited greater sexual dimorphism in height at first flowering.

4. DISCUSSION

Our study provides a novel example of how the degree of sexual dimorphism in a dioecious plant varies during the life cycle according to the timing of reproductive function of the sexes. Comparisons of seven populations of *R. hastatulus* grown under glasshouse conditions indicated that males were taller than females at first flowering, but this pattern was reversed at reproductive maturity (figure 1). Significantly, the magnitude of dimorphism at reproductive maturity

was consistent between glasshouse and field environments. We also found that variation in onset of male anthesis was associated with the degree of height dimorphism at first flowering (figure 2). We consider several hypotheses to explain these results and conclude that temporal variation in height dimorphism in *R. hastatulus* most likely reflects optimization of pollination and seed-dispersal functions.

Earlier studies reported differences between the sexes in phenology and inflorescence height of *Rumex* species. In *R. acetosella*, Putwain & Harper [8] interpreted differences in these traits as resulting from niche differentiation between the sexes owing to competition for light. In contrast, Conn [9] doubted that faster female height growth post-flowering and earlier male senescence in *R. hastatulus* resulted from niche partitioning for light. Rather, following Lloyd & Webb [1], he interpreted the differences as strategies associated with the contrasting reproductive roles of females and males. We agree with this general interpretation, but in particular consider the rapid reversal of height dimorphism as a likely adaptive response for effective pollen and seed dispersal. The absence of height dimorphism prior to the onset of reproduction in our experiment (figure 1b) is consistent with this hypothesis. Moreover, the reversal of dimorphism we observed is unlikely to be driven by competition for light as there was no relation between plant density and height dimorphism among *R. hastatulus* populations (data not shown, see also [9]).

Demonstrating that taller plants have higher fitness than shorter plants, owing to improved wind dispersal of pollen and seeds is challenging and beyond the scope of our study. However, there is sufficient theoretical and empirical evidence [1–4, 10] from other systems to support this assumption. An important consideration for species with wind-dispersed pollen and seed is height relative to surrounding vegetation [2, 4]. *Rumex hastatulus* commonly occupies monospecific stands in open areas, where plants at or above the height of the surrounding vegetation are likely to experience higher wind velocities and a greater probability of uplift

of dispersal propagules [4]. For annuals, such as *R. hastatulus*, greater seed dispersal may also be important for colonization of heterogeneous environments [6].

Could changes in height dimorphism be non-adaptive outcomes of differences between the sexes in growth and phenology related to costs of reproduction? The amount of height dimorphism at flowering was correlated with delays in male flowering, indicating that differences in phenology between the sexes contribute to sexual dimorphism (figure 2). The later male flowering we observed is unusual for a dioecious species [1], but could be associated with the need for more time to acquire resources, particularly nitrogen for the high pollen production typical of wind-pollinated species [11]. However, investment in nitrogen-acquiring roots rather than shoots might be expected under these circumstances. Alternatively, this delay may result from selection for greater stem growth to improve pollen dispersal. Greater male investment in floral structures may also result in delayed flowering and reduced height growth relative to females later in the life cycle. However, we found that females had significantly more flowers than males at reproductive maturity ($F_{1,170}$, $p < 0.001$, data not shown). It is therefore unlikely that greater male investment in floral structures is driving delayed flowering and reduced male growth later in the life cycle. In addition, females had significantly more stem biomass than males at reproductive maturity (female mean = 771.4, male mean = 678.9 mg; $F_{1,168} = 13.24$, $p < 0.001$, with height added as a covariate) presumably to assist in the support of developing fruit. Hence, despite this additional cost per unit of stem, greater female height at reproductive maturity (figure 1*a,b*) suggests a likely selective advantage of investment in taller stems for seed dispersal.

Post-flowering increase of height in females and earlier senescence of males [9] likely reflect differences in timing of their most costly reproductive activities [1]. Although the proximate mechanisms determining the sexual dimorphisms that we have investigated are poorly understood, it seems probable that they are maintained by selection given the adaptive value of plant

height for wind pollination and seed dispersal. Consequently, the reversal of height dimorphism seems likely to function in promoting pollen and seed dispersal and reflects the alternative optima required for reproductive success of the sexes.

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