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Forces Necessary to Initiate Dispersal for Three Tumbleweeds

Dirk V. Baker, K. George Beck, Bogusz J. Bienkiewicz, and Louis B. Bjostad*

Although diffuse knapweed, kochia, and Russian thistle are important tumbleweeds of the western United States, environmental factors contributing to their dispersal are not well understood. Bolting rosettes of these species were transplanted to pots and reared in a common garden to determine the affect of postsenescence water on stem strength. There were no differences in stem strength among three water treatments for Russian thistle. Kochia, under moderate water treatment, required more than twice the force to break compared to plants under the zero and high water treatments. In contrast, diffuse knapweed plants under zero water treatment required four to six times greater force to break compared to plants under the moderate and high water treatments. There was a strong difference in diffuse knapweed stem strength between field collection sites that corresponded to observed differences in proportion of plants tumbling. A wind tunnel was used to develop a conversion factor between force and wind velocity. Wind velocities necessary to break diffuse knapweed stems ranged from 16 to 37 m/s (36 to 77 mph).

Nomenclature: Diffuse knapweed, *Centaurea diffusa* Lam. CENDI; kochia, *Kochia scoparia* (L.) Schrad. KCHSC; Russian thistle, *Salsola tragus* L. SASKR, *Salsola iberica* (Sennen & Pau) Botch. ex SASKR.

Key words: Wind tunnel, soil moisture, stem strength.

The tumbleweed mechanism of dispersal is characterized when the entire above-ground portion of a senesced herbaceous plant breaks and rolls, dropping seed along the way in a wind-driven process. The point at which the plant breaks is typically at or near the soil surface. This dispersal mechanism has evolved in at least nine disparate plant families including Asteraceae, Amaranthaceae, Asphodelaceae, Brassicaceae, Boraginaceae, Chenopodiaceae, Fabaceae, Lamiaceae, and Poaceae (Becker 1978; Heyligers 1999; Roché and Wilson 1999). Despite the widespread nature of this adaptation, little research on tumbling dispersal has been published. A number of tumbleweeds including diffuse knapweed, kochia, and Russian thistle, among others, are considered noxious or invasive in much of western North America. These weeds compete with desired vegetation (Crompton and Bassett 1985; Watson and Renney 1974; Weatherspoon and Schweizer 1969) and might contribute to the spread of radioactive waste (Warren 2001). They are also anecdotally blamed for fence damage, clogged waterways, and increased fire hazard due to accumulation of plants.

Diffuse knapweed, kochia, and Russian thistle are widespread and are still spreading. For instance, diffuse knapweed was reported to infest approximately 12,000 ha (30,000 ac) in 1989 (Lacey 1989) and by 2005, over 56,000 ha (138,000 ac) were reported as infested in Colorado (Colorado Department of Agriculture 2005). Rapid response and early eradication are important components of integrated management and knowledge of the environmental conditions that are conducive to the spread of these plants could be valuable in this endeavor. For instance, the drought that has affected large areas of the west over the last several years could increase tumbleweed dispersal if dry stems were more brittle and dry soil provided a stronger fulcrum for wind force to act against. If this were true, managers should step up prevention efforts during periods of drought.

Conceptually, there are three components to tumbling dispersal. First, sufficient force must be exerted to break the main stem of plants, thereby initiating the process. Second, the plant must move across the landscape. Thirdly, seed must be retained in the plant for some distance and time. We are investigating the second and third components for diffuse knapweed in other work. However, seed dispersal of diffuse knapweed plants that do not tumble is similar to that of spotted knapweed [*Centaurea stoebe* L. ssp. *micranthos* Gugler]; seed is simply shaken out of heads to fall near the parent plant (Watson and Renney 1974). Stallings et al. (1995) investigated seed retention in Russian thistle plants with time and distance. They found that, on

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Interpretive Summary

Tumbleweeds are a diverse group of often economically important weeds that share a dispersal mechanism. Though common, this mechanism of dispersal has received little attention from researchers. This work has shown that in Colorado, soil moisture after senescence can have a strong effect on the likelihood of tumbling dispersal, although the effect is not consistent among species. Diffuse knapweed was much more likely to tumble when soil is moist. In contrast, kochia was much less likely to tumble under moderate (average) fall precipitation and Russian thistle was unaffected by soil moisture.

We used wind tunnel measurements to convert force required to break plant stems (stem strength) to wind velocities. Regardless of soil moisture, the wind velocity necessary to break Russian thistle stems was 27 m/s (61 mph) on average. Diffuse knapweed stems under dry soil conditions broke under force equivalent to winds of 32 m/s (71 mph), whereas 16 m/s (38 mph) winds were sufficient on average to break plant stems under more moist soil conditions. There are also differences in stem strength among sites for diffuse knapweed, although sites were not compared for the other species.

Kochia stems under moderate soil moisture required 50 m/s (111 mph) winds to break, whereas stems under dry or very moist conditions required 29 m/s (65 mph) winds to break. All of these estimates are weighted averages and none incorporate the fatigue effects of variable wind. Therefore, they are probably overestimates, particularly later in the fall and into the winter and early spring, when fatigue might have greatly weakened stems. These estimates can be used in assessing the vulnerability of a site to rapid spread of these species.

average, 51% of Russian thistle seed was retained in plants recovered after traveling 2,209 m (7,247 ft) in summer-fallow wheat fields in 1 yr and 26% after traveling 1,771 m (5,810 ft) in the next year. Further, they found that 61% of seed were retained on plants that did not tumble during the 6 and 12 wk of the first and second years of the study, respectively (Stallings et al. 1995). We are aware of no work addressing the second and third components of tumbling dispersal for kochia. In this work, we focused on the forces necessary to initiate dispersal.

Previous work has shown temporal and spatial variation in the tumbling dispersal of diffuse knapweed. Beck and Rittenhouse (2002) reported that the proportion of diffuse knapweed plants that tumbled during the fall and winter varied from 16 to 49% over a 3-yr study and that tumbling was reduced 9 to 37% when plants were grazed in the early summer. Nelson (2002) reported that the proportion of plants tumbling during the fall and winter varied from 45 to 70% across sites in a 1-yr study. Both of these studies were conducted near Superior, CO. We made further observations during the falls and winters from 2004 through 2006 at two sites. At a site near Superior, CO, 78% of diffuse knapweed plants tumbled on average (unpublished data). However, observations near Larkspur, CO (approximately 100 km [62 mi] south-southeast of Superior) showed only an average of 18% of plants tumbling (unpublished data).

There are undoubtedly a variety of factors and interactions that influence the strength of senesced tumbleweed stems and, hence, the likelihood of tumbling dispersal. These factors may include plant physiology, soil type, soil organic matter, stem fatigue due to varying wind direction and velocity, stem decay, solar radiation, and soil moisture. To our knowledge, the only previously published work examining the force required to initiate tumbling and related factors is that of Becker's (1978) investigation of the anatomical, histochemical, and mechanical aspects of stem abscission in kochia. He concluded that, while desiccation, anatomical changes, and decay were important factors, the physical force exerted by wind was the primary factor causing stems to break.

We had five objectives in this work. The first was to estimate the stem strength of the three species of tumbleweed (i.e., the force necessary to break the main stem at the soil surface, thereby initiating tumbling dispersal). The second was to determine the effects of soil moisture on the stem strength. The hypothesis was that increasing soil moisture would cause senesced plant stems to be more flexible and, hence, greater forces would be required to induce stem failure. Our third objective was to determine if there was a difference in stem strength between diffuse knapweed plants collected from two field sites. We hypothesized that the observed differences in tumbling dispersal at our field sites would be at least partially explained by differences in stem strength. The fourth objective was to estimate the force exerted by wind (hereafter referred to as drag effect) on diffuse knapweed. Finally, our fifth objective was to use estimated drag effect to relate stem breaking strength to wind velocity for all species.

Materials and Methods

Sites, Collection, and Rearing. Bolting rosettes of diffuse knapweed, kochia, and Russian thistle were collected and transplanted into 3.8 L (1 gal) pots with their native soil in early June of 2004 and 2005. Bolting rosettes were used to control for the unpredictability of whether a diffuse knapweed plant grown from seed or rosette would bolt and bloom in a given year. Diffuse knapweed plants were obtained from a site near Larkspur, CO and from a site near Superior, CO. Forty-five plants were collected from each site in 2004 and 65 in 2005. Kochia and Russian thistle plants were collected from agricultural fields within Colorado State University's Agricultural Research, Demonstration, and Education Center (ARDEC, Fort Collins, CO). Twenty-five kochia and Russian thistle plants were collected in 2004 and 45 in 2005. Potted plants were placed into 46-cm- (18-in-) high wood frames and wood mulch was packed between pots to minimize the potential effects of temperature fluctuation on root growth. Plants

were maintained outdoors under drip irrigation at ARDEC and monitored to ensure they were receiving sufficient water to prevent wilting. At the onset of senescence (late August), plants were transferred indoors and allowed to complete senescence with no further water added.

A weather station¹ equipped with an anemometer and directional vane was placed at each site from late September, 2004 through March, 2005 and for the same period the following season.

Treatments. After plants senesced, each was assigned to a postsenescent water treatment in a completely random design. A minimum of 10 plants was assigned to each water treatment per year based on a simple power calculation and available greenhouse space for watering. Due to small 2004 sample size, there were two treatments: water and no-water. Plants assigned to the water group received 145 ml (4.9 oz) of water two times per week for 8 wk, and those in the no-watered groups received no water for the same period. More plants and space were available in 2005; therefore an additional water level was added and a minimum of 20 plants of each species was assigned to this treatment. Plants assigned to the highest water level treatment received 145 ml every 2 d for the 8-wk postsenescence period. The moderate level of water (145 ml, twice per week) was based on the 55-yr average precipitation during September and October for the collection sites (about 5 cm [2 in] per month). Separate groups of diffuse knapweed plants were randomly selected for the site difference trials and wind tunnel tests. The ultimate sample size (n) for each treatment is shown in Table 1. Sample sizes within treatment were roughly equal between years.

Measuring Breaking Strength. At the end of the 8-wk treatment period, the horizontal force necessary to induce stem failure was measured. Failure was defined as the point at which the plant stem broke and the plant could freely tumble. Measurements were completed within 3 d of the cessation of treatments and plants within species were measured within a few hours of each other. Horizontal force was measured with a device composed of a vertical beam, crank, pulley, and a tubular scale. The pulley was mounted to the beam and was adjustable in height to insure force exerted was horizontal. A 13.6 kg test weight (30 lb) line was attached from the crank through the pulley to the scale. A short piece of line was wrapped around the plant stem and attached to the other end of the scale. The point of attachment was a visually estimated, vertical coordinate of the centroid of the plant canopy—an approximation of the center of the wind shadow of each plant. The crank was then used to gradually increase the horizontal force exerted on the plant until the plant stem failed. Stem failure typically occurred at or near the soil surface. The force, rounded to the nearest 0.01 kg, and the height (cm) on the stem at which the line was attached were

both recorded. The measured force was multiplied by the height of attachment to calculate the breaking moment (M_B), which was the dependent variable for this analysis. The plant size was characterized by the canopy diameter (at its widest) and the stem diameter (at the soil surface). These diameters were measured as possible covariates for analysis.

Estimating Drag Effect. A wind tunnel was designed and constructed to carry out investigations under controlled wind conditions. This wind tunnel was capable of generating air flow velocities from 0 to 8 m/s (0 to 18 mph). Air flow was monitored with a hot-film probe, in conjunction with a constant temperature anemometer.² The test section of the tunnel was equipped with a proximity sensor³ calibrated to monitor wind drag effects on a plant. The output from this sensor was logged to a personal computer and was sampled at 1-s intervals. Thirty samples were used to calculate the temporal average of the acquired data. Output voltage ranged from 0.000 to 10.000 DCV over a calibration proximity range of 3 mm (0.12 in), thereby giving proximity accuracy to 3 μ m (1.2×10^{-4} in). The proximity was the distance between the sensor and a sensor target, a metal plate that was spring-mounted and furnished with a mount employed to test (individual) plants. Given that force is directly proportional to change in proximity, this device was calibrated to provide information on wind drag (force) exerted on a plant. During calibration, known force was applied to the system using the same device used to measure stem strength. During wind tunnel experiments, the proximity was measured for calm and with wind (3.3 m/s [7.4 mph]) conditions and the difference in proximity was converted into the drag force, using the calibration conversion factor. This factor is analogous to, for instance, the conversion factor between Kg-m and N-m. This methodology of using a scale to measure force then using a proximity sensor in conjunction with a wind tunnel to convert that force to a wind velocity is based on those of Kawakita et al. (1992) who estimated forces exerted on a roof by wind.

Measurements were carried out for each diffuse knapweed plant. Kochia and Russian thistle were not included in this experiment because it was not feasible to construct a wind tunnel large enough to accommodate these species. The wind velocity selected for testing was chosen to represent moderate wind conditions and to ensure repeatability of wind tunnel measurements. The following equation relates the aerodynamic overturning moment to the wind speed U and the remaining principal independent variables:

$$M_B = (1/2\rho U^2)C_M A\sqrt{A} \quad [1]$$

where M_B is the overturning moment associated with stem breaking, ρ is air mass density (approximately

Table 1. Force and calculated wind velocities necessary to break tumbleweed stems in a single event (SE = standard error; n = sample size).

Species	Force ^a	SE	n	Calculated wind
	<i>lnkg·cm</i>			<i>m/s (mph)^b</i>
Diffuse knapweed				
Larkspur	2.42a	0.09	46	34.2 (76.5)
Superior	1.97b	0.09	47	27.3 (61.1)
Diffuse knapweed				
0 H ₂ O ^c	2.65a	0.21	16	37.4 (77)
M H ₂ O	0.97b	0.19	20	16.1 (36)
H H ₂ O	1.04b	0.21	16	16.7 (37.4)
Kochia				
0 H ₂ O	3.24a	0.23	22	31.9 (71.4)
M H ₂ O	4.12b	0.25	20	49.6 (111)
H H ₂ O	2.78a	0.27	17	25.4 (56.8)
Russian thistle				
0 H ₂ O	2.62a	0.32	16	27.5 (61.5)
M H ₂ O	2.71a	0.32	16	28.8 (64.4)
H H ₂ O	2.54a	0.25	26	26.5 (59.3)

^a Different lower case letters denote significant differences at $\alpha = 0.01$. Comparisons were made only within species and, in the case of diffuse knapweed, separately for the site and water experiments. Due to small sample size, we did not make site comparisons within water treatment. Lsmeans are reported for diffuse knapweed.

^b Wind calculations for kochia and Russian thistle assume that the plant characteristics that predict drag effect are similar to those for diffuse knapweed.

^c Water treatments for the eight week treatment period: 0 H₂O, no water; M H₂O, 145 ml (XX tsp) 2 times per wk; H H₂O, 145 ml (XX tsp) every 2 d.

1.066 kg/m³ [0.067 lb/ft³] at 1,500 m [4,921 ft] elevation (Lide 1992–1993)), U is wind speed, C_M is the moment coefficient and $A\sqrt{A}$ is volume, and A is a reference area. Because the purpose of this work was to relate wind speed to the breaking moment (force), there was no need to uniquely estimate the moment coefficient and volume or area. In fact, determining these parameters would be problematic because volume in the equation refers to solid volume. Hence, these variables can be combined as is expressed in Equation 2, where Ψ is the product of the moment coefficient and volume, hereafter referred to as wind drag effect parameter, or drag effect.

$$M_B = (1/2\rho U^2)\Psi \quad [2]$$

Analysis. Data were \ln transformed to meet assumptions associated with normal distribution of residuals and subjected to ANOVA with covariates and regression using SAS v9.1 (Proc GLM, SAS Institute 2005). Collection site, canopy diameter, and stem diameter were the covariates included for soil moisture effects and for evaluating site differences. The regressors for the analysis of drag effect were plant height, canopy diameter, and plant weight. The

experimental unit was an individual plant. Backward model selection was used and began with inclusion of all main effects and two-way interactions. Effects were eliminated by lack of significance or estimability due to sample size. Means were expressed as lsmeans where applicable.

Results and Discussion

Water Effects on Stem Strength. The model including all three species showed no year effect and a strong water by species interaction ($P < 0.0001$). Therefore data were pooled over the 2 yr of the study and analyses conducted by species.

Water treatment had no influence on Russian thistle stem strength ($P = 0.915$) and was the only significant effect for kochia ($P = 0.0015$) (Table 1).

For diffuse knapweed, collection site ($P = 0.0121$), water treatment ($P < 0.0001$), and the interaction between site and stem diameter ($P = 0.0356$) were significant effects. Although stem diameter was not a significant main effect ($P = 0.1066$), it was included in the model due to the interaction. The mean (\ln) breaking strengths (\pm SE) for diffuse knapweed from Sites 1 and 2 were 1.91 kg cm

(± 0.2) and 1.29 kg cm (± 0.22), respectively. Site comparisons within water treatment were not conducted due to insufficient sample size.

Our hypothesis that stem strength would increase with increasing soil moisture was based on three premises. First, moist soil is soft and provides less of a fulcrum for the wind (or force) to act upon. Second, moisture absorbed from the soil by stems would cause the stems to be more flexible. Third, it could be hypothesized that long-distance dispersal would be more adaptive when the local habitat is least suitable. If the immediate locale of the parent plant is very dry, it is not well-suited to seedling establishment and survival, therefore it might be more adaptive for seeds to be dispersed over greater distances. However, this hypothesis was not supported for diffuse knapweed or Russian thistle and only partially supported for kochia due to the similarity of the zero and high water treatments (Table 1).

Site Effects on Diffuse Knapweed Stem Strength. The experiments to determine the basis for observed site differences in tumbling dispersal showed that stem strength depended on site ($P = 0.0005$) and stem diameter ($P < 0.0001$) and that the effect of stem diameter was not dependent on site ($P = 0.9042$). On average, plants from the Larkspur site required 57% more force (back-transformed data) to break than those from Superior (Table 1). However, only 32% of the variance in stem strength was explained by the model that included site and stem diameter as parameters. Stem diameter depended on site ($P = 0.0397$). The average diameter (\pm SE) of Larkspur plant stems was 5.5 mm (± 0.2) (0.22 in) and 5 mm (± 0.2) (0.2 in) for Superior plant stems. However, the small difference in stem diameter between sites and the low R^2 suggest that there are other factors involved. Further, the question of why there is a difference in stem diameter between sites remains. Although we did not measure soil texture and we did not observe a strong difference in soil texture between the sites, it might provide some explanation of the site difference in stem strength. Clearly the soil texture is important in the strength of the fulcrum it provides for wind to act against.

We noted two important differences between the sites that might provide some explanation of the difference in stem strength. First, there seemed to be putative hybrids between diffuse knapweed and spotted knapweed at Larkspur but not at Superior. It seems reasonable that hybridization with a plant that does not disperse via the tumbling mechanism might increase the stem strength of progeny. Spotted knapweed has not been reported to disperse by tumbling. A test of this hypothesis controlling for stem diameter showed no difference ($P = 0.9924$) in stem strength between diffuse knapweed plants and putative hybrids within the Larkspur site, thus refuting

Table 2. Drag effect regression parameter estimates for postsenescence diffuse knapweed plants collected from two sites in Colorado in 2004 and 2005. Drag effect, or the force exerted by wind on a plant, was estimated using a wind tunnel and \ln transformed for analysis.

Parameter	Estimate	SE	P value
Intercept	-5.551	0.2838	< 0.0001
Height	0.058	0.0069	< 0.0001
Weight	0.108	0.0146	< 0.0001
Height \times Weight	-0.002	0.0003	< 0.0001

this hypothesis. However, because there were only nine putative hybrids, this result is tentative and further research is needed to determine the possible effects of hybridization.

Second, 33 of the 47 plants from Superior that we reared from the bolting stage showed symptoms of damage by the root-borer biological control agent *Cyphocleonus achates*. There was no evidence of this damage on plants from Larkspur. The larvae of this biocontrol agent are root-borers. Because the damage caused by these larvae is proximate to the location at which we observed most of the noninfested plants breaking, it is likely that this damage could further weaken the plants, making them more likely to tumble. Our test comparing the infested and non-infested plants within the site showed no effect ($P = 0.7881$) controlling for stem diameter, refuting this hypothesis. However, we are again limited by sample size and this potential effect of the biocontrol agent on dispersal warrants further investigation. It would indeed be ironic if a promising biological control agent increases long-distance dispersal of the plant.

Drag Effect. Analysis of drag effect estimates showed that the drag effect (\ln transformed) depended on plant height ($P < 0.0001$), plant weight ($P < 0.0001$) and their interaction ($P < 0.0001$) (Table 2, $R^2 = 0.796$). These are fairly intuitive results, particularly if we consider the weight of the plant to represent the density of the plant structure. It was surprising, however, that the plant canopy diameter was not significant ($P = 0.976$, slope = -0.00015), because we expected that the height and canopy would describe the plant profile with which the wind interacts.

With the estimated drag effect and Equation 2, we calculated the wind velocity equivalents of breaking forces (Table 1). For diffuse knapweed, plants in dry soil required more than twice the wind velocity to break than did those under moist soil conditions. Kochia plants under moderate soil moisture conditions required approximately 73% greater wind to break than the other two treatments. Calculations for kochia and Russian thistle assume that the plant characteristics that dictate drag effect (i.e., height, weight, and their interaction) are similar to those for

Table 3. Wind observations at two sites in Colorado. Observations were made from late September, 2004 through March, 2005 (denoted 2004) and late September, 2005 through March, 2006 (denoted 2005).

Site	Year	Sustained winds (m/s)		Gusts (m/s)	
		Avg.	Range weekly max	Avg.	Range weekly max
Larkspur	2004	3.8	8.4 to 21.9	6	11.7 to 30.8
	2005	4.2	7.2 to 20.6	6.4	10.4 to 32.8
Superior	2004	3.2	4.6 to 24.1	5.2	8 to 36.9
	2005	3.4	3.5 to 22.5	5.7	5.6 to 35.6

diffuse knapweed. Hence, the wind velocities reported for kochia and Russian thistle should be taken only as rough approximations.

The generalization of our results is limited by several factors. We conducted our tests 8 wk after plants senesced. Although this time period was based on field observations of dispersal timing, it is somewhat arbitrary. It is likely that stem strength varies with time after senescence, even within our chosen treatments. We also kept soil moisture reasonably constant and soil moisture fluctuation might also have an important effect. Because our tests consisted of gradually increasing, unidirectional force, the effects of fatigue due to variability in wind velocity and direction are not reflected in our data and could dramatically reduce stem strength over time. Wind in the field is turbulent and highly variable, even over relatively short time periods. This factor might substantially affect stem strength. However, the calculated wind speeds necessary to break plant stems are largely within the range of wind gusts observed at our field sites (Table 3). Arguably, it is wind gusts that are most important for fatiguing and breaking plant stems. Finally, soil characteristics such as texture and organic content, as well as decay of the root and lower stem could be important, but were not measured in this work.

Despite these qualifications, it is clear that soil moisture has a strong effect on the stem strength of both diffuse knapweed and kochia. These results suggest that long-distance dispersal of diffuse knapweed could be increased during autumns of high soil moisture compared to dry autumns. Further, the moisture would facilitate germination and seedling establishment. In contrast, long-distance dispersal of kochia might be increased during autumns characterized by low or extreme soil moisture. Awareness of the environmental conditions that are well-suited for dispersal of these plants can be an important management tool. For instance, sites that experience higher moisture in the fall as well as strong winds might be particularly prone to long-distance dispersal of diffuse knapweed, whereas drier or extremely wet sites might maximize kochia dispersal. These data can also be used to assess the vulnerability of sites to rapid dispersal and infestation by tumbleweeds.

There are several aspects of this work that should be further investigated. Becker (1978) and Zeroni et al. (1978) reported on the physiological basis for stem failure that characterizes the tumbleweed mechanism of dispersal in the *Kochia* genus and Becker (1969) for *Psoralea*. Similar work is needed for diffuse knapweed and Russian thistle. This work would be of particular interest for diffuse knapweed given the temporal and site-based variation in the proportion of tumbling vs. nontumbling plants shown in our observations and by Beck and Rittenhouse (2002) and Nelson (2002).

Sources of Materials

¹ Hobo, Onset Computer Corp., 470 MacArthur Blvd., Bourne, MA 02532.

² Hotwire anemometer, model 407123, Extech Instruments, 285 Bear Hill Rd, Waltham, MA 02451-1064.

³ GageProx 8 mm unshielded proximity sensor, Kaman Instruments, Kaman Aerospace Corporation, Measuring Systems Group, 13 South Tejon, Suite 303, Colorado Springs, CO 80903.

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