

PROBLEMS OF POPULATION STRUCTURE EXEMPLIFIED BY THE INVASIVE TROPICAL SHRUB *PARKINSONIA ACULEATA* L. IN NORTHERN AUSTRALIA**A.C. Grice^{1,2,6}, S.D. Campbell^{3,6}, J.R. McKenzie³, L.V. Whiteman², M. Pattison³, K. Headricks⁴ and M.H. Andrew⁵**¹ *Corresponding author*² *CSIRO Sustainable Ecosystems, Private Bag P.O. Aitkenvale, Queensland, Australia 4814
Telephone: 07-4753 8543, Facsimile: 07-4753 8600, Email: tony.grice@csiro.au*³ *Tropical Weeds Research Centre, Queensland Department of Natural Resources, Mines and Energy, P.O. Box 187, Charters Towers, Queensland, Australia 4814*⁴ *17 Townsend St, Mysterton, Queensland, Australia 4814*⁵ *URS Sustainable Development, 25 North Terrace, Hackney, Adelaide SA 5069 Australia*⁶ *CRC for Australian Weed Management, PMB1 Waite Campus, Glen Osmond, South Australia, Australia 5064***Abstract**

Age-class frequency distributions are valuable means of describing plant populations because they can be used to infer population history. Variables other than age are also often used to describe plant populations, either because they more accurately reflect an attribute of interest, or because it is difficult to determine age. However, interpretation of frequency distributions based on variables other than age can be problematic. We discuss these problems and illustrate them using data from six populations of the invasive rangeland shrub *Parkinsonia aculeata* L. We used three different measures of plant size: height, canopy diameter and stem cross-sectional area. Structures based on these measures were compared with structures based on three different estimates of above-ground biomass derived from them. For each variable, structures differed greatly between populations, and for each population, they were strongly dependent on the variable used to describe it. Population structures based on three-dimensional variables (above-ground biomass) tend to be more strongly positively skewed than those based on two-dimensional (area) measures of plant size. These in turn are more strongly positively skewed than those based on one-dimensional (height, diameter) measures. The statistical basis of this general phenomenon is discussed. The results highlight the difficulties of deriving histories and projecting futures of populations from size-class frequency distributions without accompanying knowledge of the temporal patterns of change in size variables as plants grow.

Keywords: *Parkinsonia*, population structure, shrubs, weeds.

Introduction

The structure of populations of woody perennials is usually described in terms of the proportions of individuals that are assigned to different classes at a point in time. Often this is done using plant age, so yielding age-class frequency distributions. Age-class frequency distributions are useful because they can be used as a basis for implying what the history of a population has been or to suggest what the future trends are likely to be, although these interpretations depend upon either knowledge or assumptions about age-specific recruitment and mortality rates (Silvertown 1982).

Often, plant population structures are described in terms of variables other than age. This may be because variables other than age more accurately reflect an attribute of interest. For example, for many plant species, the size of plants may be better than age as a predictor of demographic characteristics such as seed production. Alternatively, variables other than age may be used because it is easier or less time-consuming to measure them than to estimate age. In many cases, it is not possible to determine the age of plants by conventional means such as counting growth

rings (Coleman and Ireland 1995). This often applies, for instance, to species that grow in areas with variable climates, where growth rings are not laid down on an annual basis.

Variables other than age that have been used to describe plant population structures include qualitatively defined life-stages (Watson *et al.* 1997) and various measures of plant size. One commonly used measure of size is diameter at breast height (dbh), which is used to describe the population structures of tree species because this variable is correlated with timber yields, the primary interest of foresters (e.g. Ter-Mikaelian and Korzukhin 1997). Height is a commonly used measure of plant size in shrub species (Auld 1995, Watson *et al.* 1997) but equally valid possibilities include canopy diameter, stem diameter and stem circumference (Auld 1995).

Above-ground biomass can also be used as a basis for describing population structures. This variable has the advantages that it is less likely to be sensitive to plant shape and probably more reliably reflects demographic responses. On the other hand, biomass of individuals growing in natural populations cannot be measured directly without destructive sampling; indirect measures require double sampling. The choice of variable must be based on the ease with which it can be measured and how closely it reflects the patterns and processes that are of interest.

Whatever the measure used, it has been common practice to interpret size-class frequency distributions as if they were age-class frequency distributions and to use them to imply population history or suggest future trends (Lange 1966, Barbour 1969, Crisp and Lange 1976, Crisp 1978, Auld 1995). One can be confident about such interpretations only when there is a known relationship between size and age (Grice *et al.* 1994, Watson *et al.* 1997). Moreover, it is important to consider how the shape of size-class frequency distributions may depend upon the measure of size and the class intervals that are used.

In this paper we consider how the class frequency distributions that are used to describe the structure of a population are influenced by the variable chosen as a surrogate for age. We demonstrate the effect of the variable chosen using data from six Australian populations of the shrub *Parkinsonia aculeata* L. (parkinsonia, Jerusalem thorn, Caesalpiniaceae). We compare population structures of *P. aculeata* derived using three different measures of plant size and three different estimates of above-ground biomass.

Parkinsonia aculeata is an invasive species in Australian rangelands being widespread and abundant in Western Australia, the Northern Territory and Queensland. Scattered populations occur in New South Wales and South Australia. It is a declared weed in each of these states (Parsons and Cuthbertson 1992).

Methods

Six study sites (sites 1-6) were selected on cattle properties in north-eastern Queensland (Table 1). Together they covered a range of landscape positions and densities of stands of *P. aculeata*, although they represent only a small proportion of the Australian range of the species. Accessibility was an important criterion. Sites 1-4 were south of Charters Towers in the catchment of the Cape River. Sites 5 and 6 were between Prairie and Hughenden in the upper reaches of the catchment of the Flinders River.

Table 1. Locations, areas surveyed, number and density of plants for six sites in north-east Queensland.

Site	Latitude	Longitude	Area (ha)	No. of plants	Density (per ha)
1	21°0'S	146°21'E	0.0172	83	4826
2	21°0'S	146°22'E	5.74	191	33
3	21°2'S	146°33'E	0.15	85	567
4	21°2'S	146°32'E	0.216	73	338
5	20°52'S	144°27'E	1.563	61	39
6	20°53'S	144°27'E	0.0767	60	782

A single rectangular plot was selected at each site. The size of each plot was determined in relation to the density of *P. aculeata* at the site, so that at least 60 plants were included in each plot. All plants within each plot were measured and the area of the plot was recorded.

The height, canopy diameter and stem diameters of each plant were measured using the method of Grice *et al.* (2002):

- (i) height (H) – measured with an accuracy of ± 0.05 m;
- (ii) canopy diameter (D_1, D_2) – measured in two orthogonal directions (north-south, east-west) with an accuracy of ± 0.05 m;
- (iii) stem diameter (d_1, d_2, d_3 etc, depending on the number of stems) measured at a height of 0.2 m above ground level, along a north-south axis using calipers, and recorded with an accuracy of ± 0.5 mm.

Mean canopy diameter was derived as:

$$D = (D_1 + D_2)/2.$$

By assuming stems were circular in cross-section, total stem cross-sectional area (A , cm^2) was calculated as:

$$A = \pi[(d_1/2)^2 + (d_2/2)^2 + (d_3/2)^2 + \dots].$$

For each plant, three estimates of above-ground dry weight (W) were made using size-biomass relationships that were established using data collected from eight Australian populations of *P. aculeata* (Grice *et al.* 2002; Table 2). The sites used in this study were the Queensland sites identified in Grice *et al.* (2002). The three estimates of above-ground dry weight (hereafter referred to as “biomass”), based on plant height, canopy diameter and stem cross-sectional area will hereafter be distinguished as W_H, W_D, W_A respectively.

Population structures were described by allocating the plants in each population to size and biomass classes. In each case, twenty classes were used. Hereafter, classes are identified by the upper limit of the class. For biomass, the presence of plants estimated to weigh more than 60 kg is indicated by the use of a 60+ kg class, which includes all plants estimated to weigh more than 57 kg. Less than 1% of plants fell into this category.

To demonstrate the general effect of dimensionality on population structure, an artificial data set was created. Five hundred random numbers ($0 < x < 20$; $n = 500$) were taken to represent a linear dimension that is a measure of plant size, for example, plant height, canopy diameter or stem diameter. The square of each number was calculated and taken to represent a two-dimensional measure of plant size such as the projected cover of the canopy or stem cross-sectional area. The cube of each number was calculated and taken to represent a three-dimensional measure of plant size, such as plant volume or biomass. The frequency distributions of these three sets of numbers were then compared.

Results

Population structure of P. aculeata

The frequency histograms used to describe the structures of populations of *P. aculeata* show considerable variation in form. For each of the measures used, frequency distributions differ greatly between populations, but for each population, the structure also varies considerably depending on the variable that is used to describe it.

Five of the six populations have height class frequency distributions in which there are relatively

few plants less than 1 m high (Fig. 1). Most populations are numerically dominated by plants 150–450 cm high and have only a small proportion of plants more than 500 cm high (Fig. 1a, c-f). Only the population at site 2 is numerically dominated by plants less than 100 cm high (Fig. 1b).

Four of the six populations (sites 1-4) have diameter class frequency distributions with a relatively high proportion of plants in the 50 cm and 100 cm mean canopy diameters classes (Fig. 2a-d). The other two populations are dominated by plants with canopy diameters of 200–500 cm (Fig. 2e,f).

Populations at sites 1-4 are numerically dominated by plants in the two lowest stem cross-sectional area classes having fewer than 30% of individuals in higher classes (Fig. 3a-d). In populations at sites 5 and 6 the modal stem cross-sectional area class was the second lowest class but at least 60% of plants were in higher classes (Fig. 3e-f).

For each site the three different estimates of biomass yielded population structures that were very similar to one another. This is in spite of the fact that height is not as reliable a predictor of biomass as canopy or stem diameter (Table 2). Regardless of which estimate of biomass was used, populations at sites 1-4 were numerically dominated (42–100% of individuals) by plants in the lowest biomass class (<3kg) (Figs 4-9). At sites 5 (Fig. 8) and 6 (Fig. 9), less than 35% of plants were estimated to be in this lowest class. Only at site 5 was a proportion of the population in the upper biomass class (>57kg) estimated to be greater than 5% (Fig. 8).

Table 2. Relationships between three variables [height (H, m), canopy diameter (D, m), stem cross-sectional area (A, cm²)] and above-ground biomass (W, kg) of *P. aculeata* derived from data collected at eight sites (Grice *et al.* 2002).

Variable	Equation	R ²
Height	(1) $W_H = 0.025H^{4.47}$	0.74
Canopy diameter	(2) $W_D = 0.091D^{3.64}$	0.86
Stem cross-sectional area	(3) $W_A = 0.022A^{1.61}$	0.92

Artificial data

The frequency distributions of x , x^2 and x^3 differed greatly from one another. Figure 10 demonstrates a relatively even distribution of the initial random numbers (x) across the ten frequency classes, but that the frequency distributions of x^2 and x^3 are strongly positively skewed. A positively skewed distribution is one in which the longer tail is to the right.

Discussion

The structures of populations of *P. aculeata*, as expressed in frequency distributions of one-dimensional measures of size (height, canopy diameter), vary considerably from site to site. Among the six stands examined in northeastern Queensland, there were three general patterns (Figs 1 and 2):

- (i) populations that were numerically dominated by small plants and in which successively higher classes had progressively fewer members (Type I);
- (ii) populations with only a small proportion in the lower and upper size-classes and numerically dominated by medium-sized plants (Type II);
- (iii) populations with multi-modal structures (Type III).

Conventional interpretations of these distributions, based on the assumption that peaks in size-class frequency distributions correspond to episodes of recruitment, would be that in Type I populations there has been recent large-scale recruitment; in Type II populations there has

been a dearth of recent recruits; and in Type III populations there has been a series of episodic recruitment events with the cohorts arising from them remaining distinguishable from one another during their subsequent development.

However, comparison of the structures derived using different measures of plant size brings these interpretations into question. For example, the three structures derived for site 1 using different measures of plant size are quite different in form. The height-class frequency distribution is Type II, with only a small proportion of plants being less than 100 cm high and most plants being between 100 and 500 cm high (Fig. 1a). The canopy diameter-class frequency distribution is Type III, with the greatest proportional representation in the 50 cm, 250 cm, 300 cm and 450 cm diameter classes (Fig. 2a). The frequency distribution of stem cross-sectional area is Type I, with almost 80% of plants being in the two lowest classes (Fig. 3a). Site 5 shows similar variation between the structures based on the different measures of plant size. Its height-class distribution is Type II, being strongly dominated by plants between 300 and 450 cm high (Fig. 1e). The canopy diameter distribution is tri-modal but with most plants being in the middle classes (250-500 cm) (Fig. 2e). The frequency distribution of stem cross-sectional area has fewer plants in successively higher classes (Type I) (Fig. 3e). The other four sites show comparable variation (Figs 1-3).

Figure 1

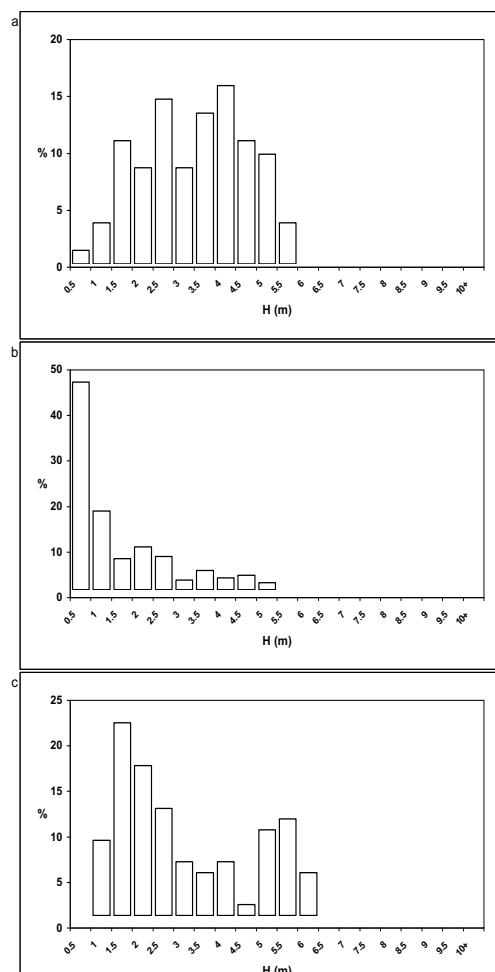


Figure 1 (cont.)

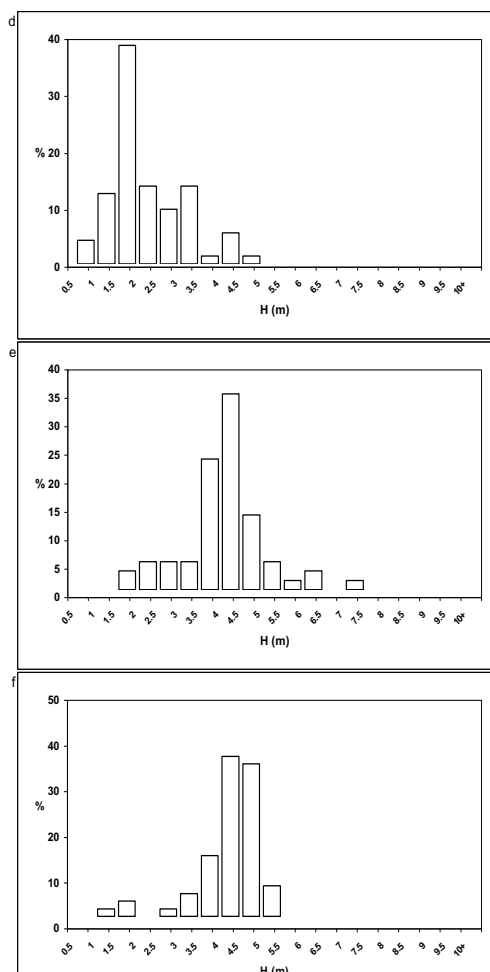


Fig. 1. Frequency distribution of height for (a) site 1; (b) site 2; (c) site 3; (d) site 4; (e) site 5; (f) site 6.

Figure 2

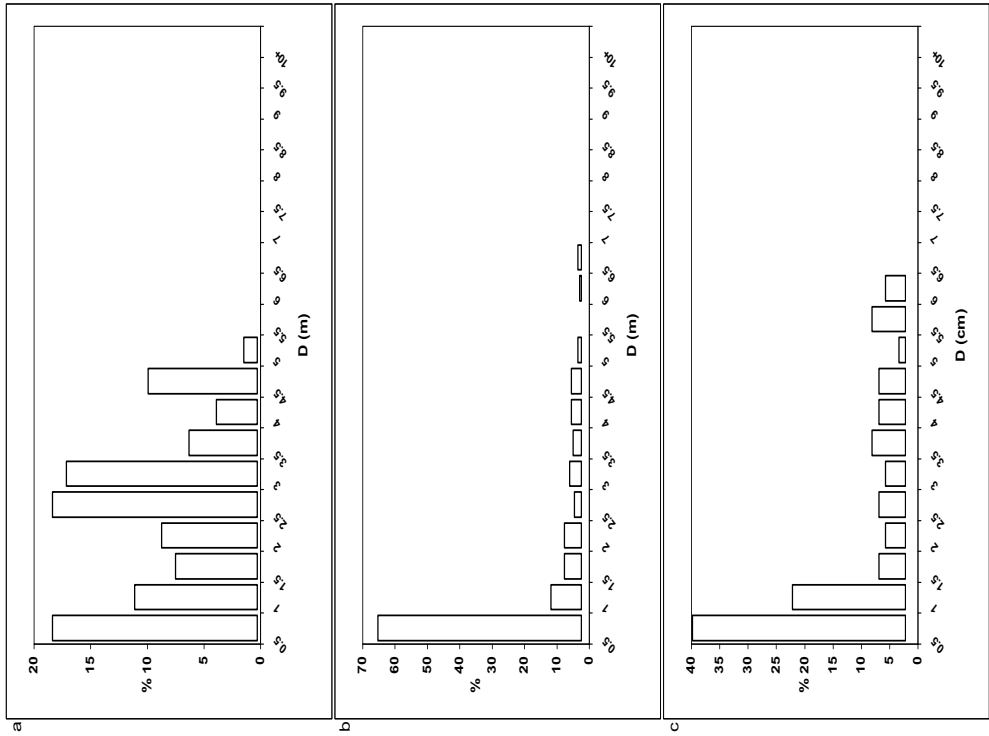


Figure 2 (cont.)

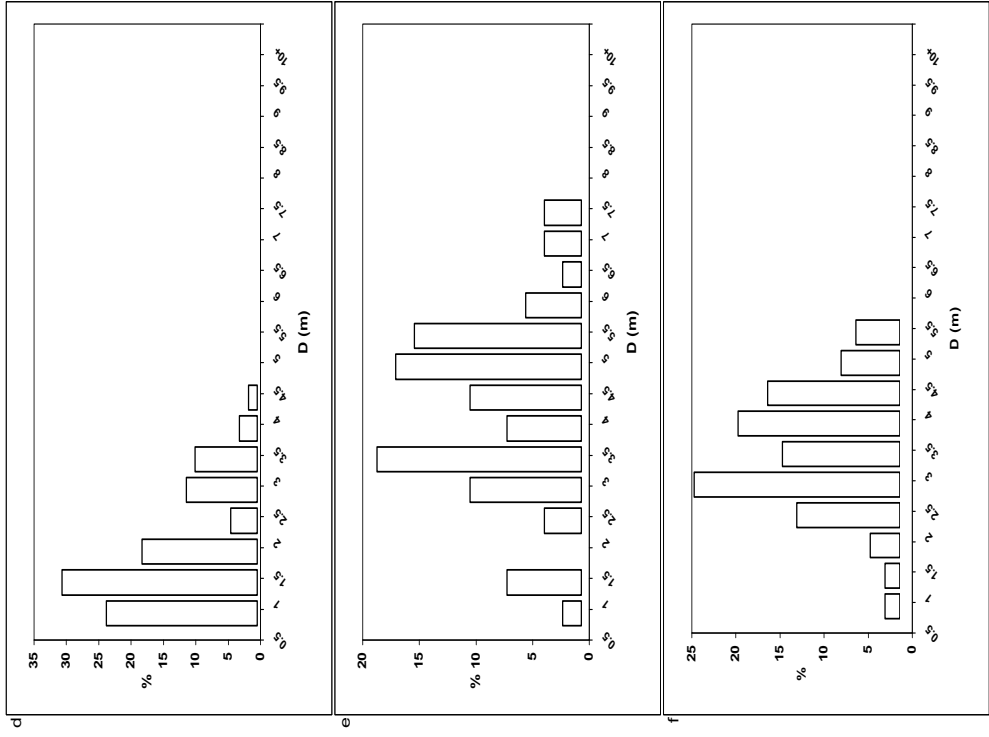


Fig. 2. Frequency distribution of canopy diameter for (a) site 1; (b) site 2; (c) site 3; (d) site 4; (e) site 5; (f) site 6.

Figure 3

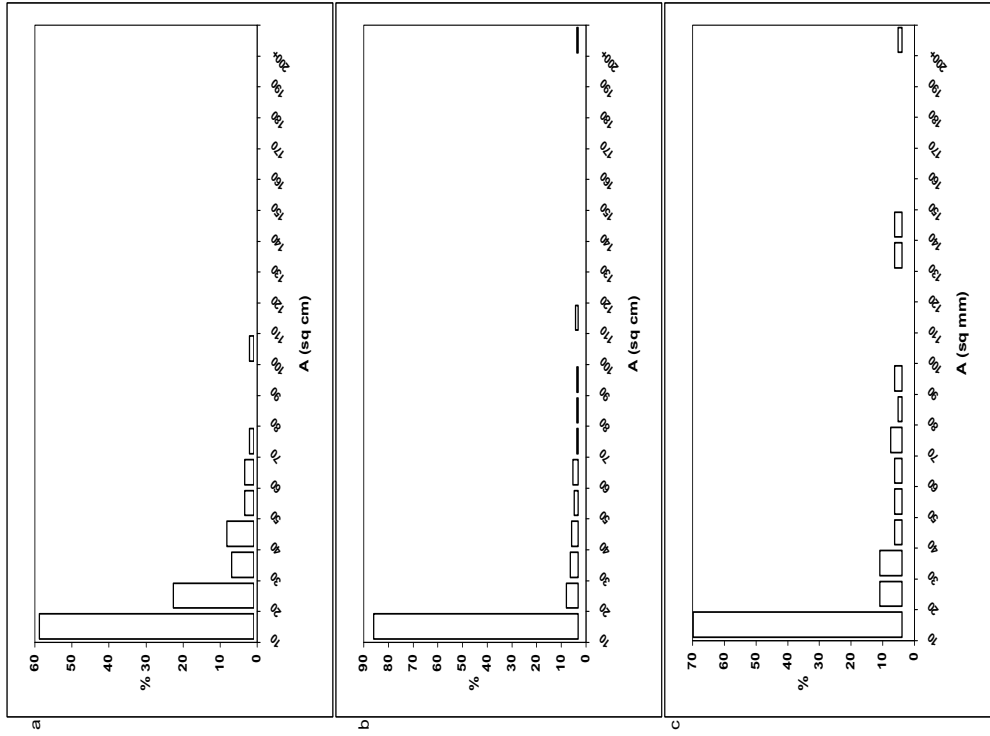


Figure 3 (cont.)

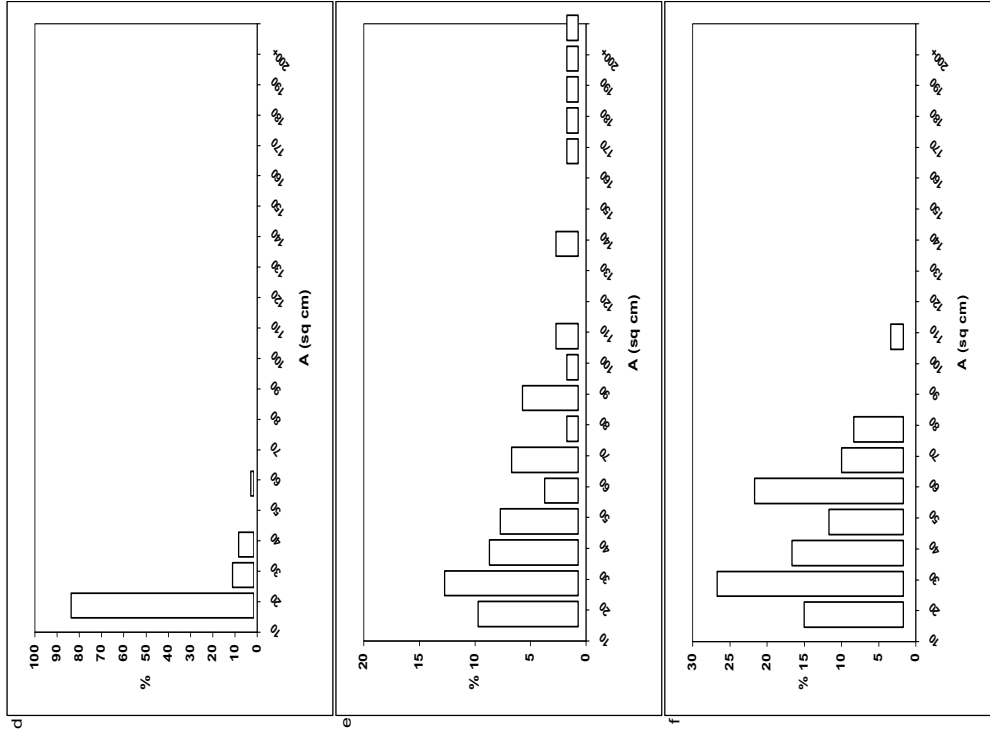


Fig. 3. Frequency distribution of stem cross-sectional area for (a) site 1; (b) site 2; (c) site 3; (d) site 4; (e) site 5; (f) site 6.

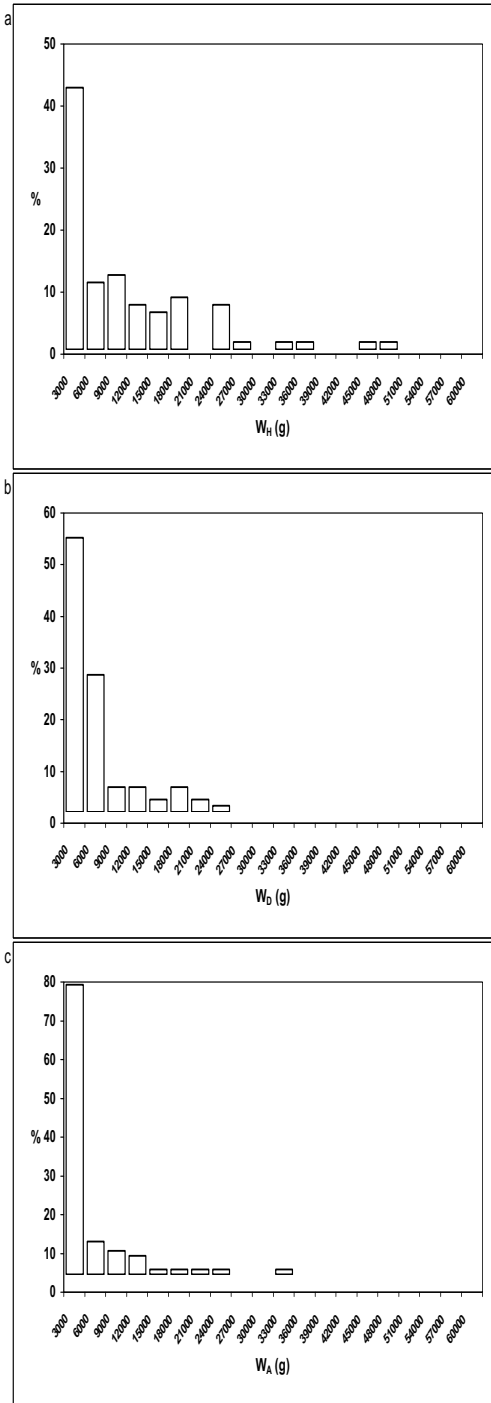


Fig. 4. Biomass-class frequency distributions for site 1 based on three different estimates of above-ground dry weight (a) W_H ; (b) W_D ; (c) W_A .

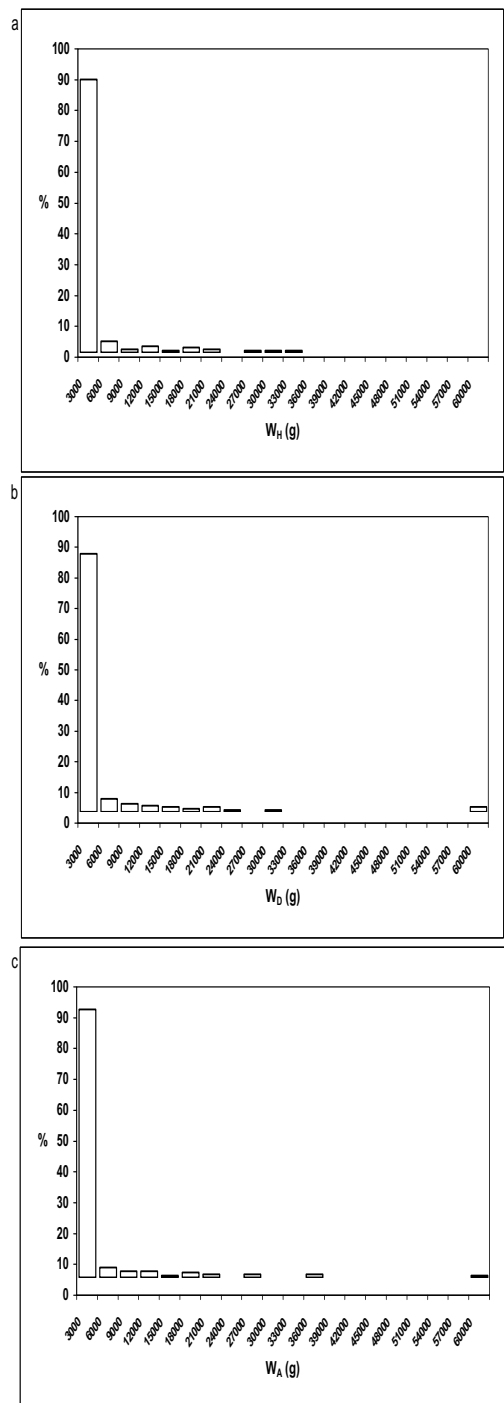


Fig. 5. Biomass-class frequency distributions for site 2 based on three different estimates of above-ground dry weight (a) W_H ; (b) W_D ; (c) W_A .

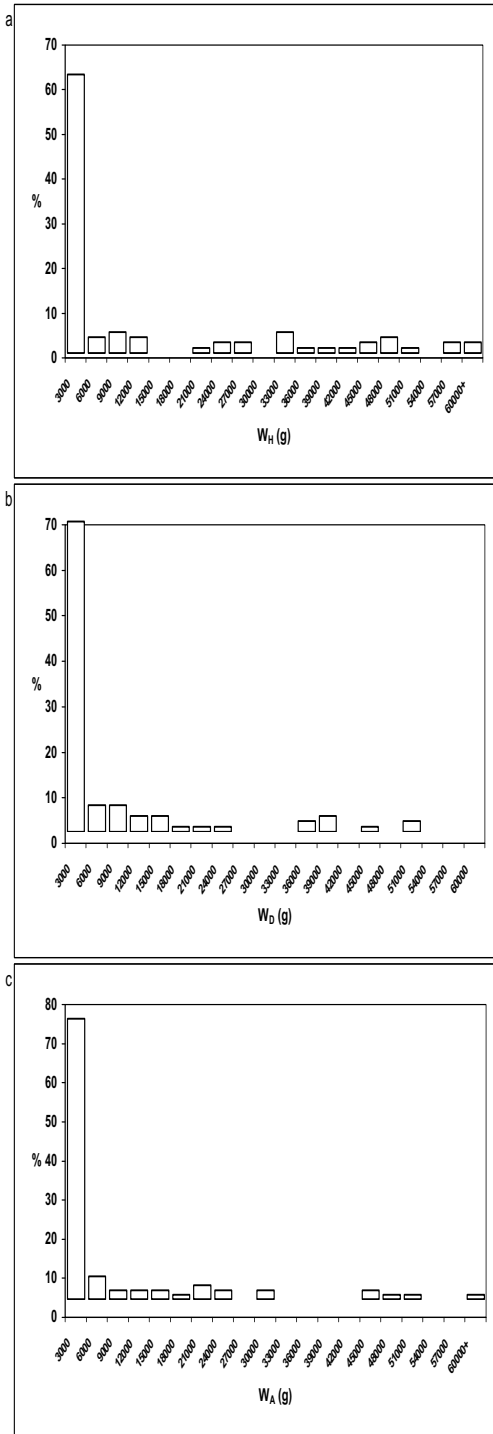


Fig. 6. Biomass-class frequency distributions for site 3 based on three different estimates of above-ground dry weight (a) W_H ; (b) W_D ; (c) W_A .

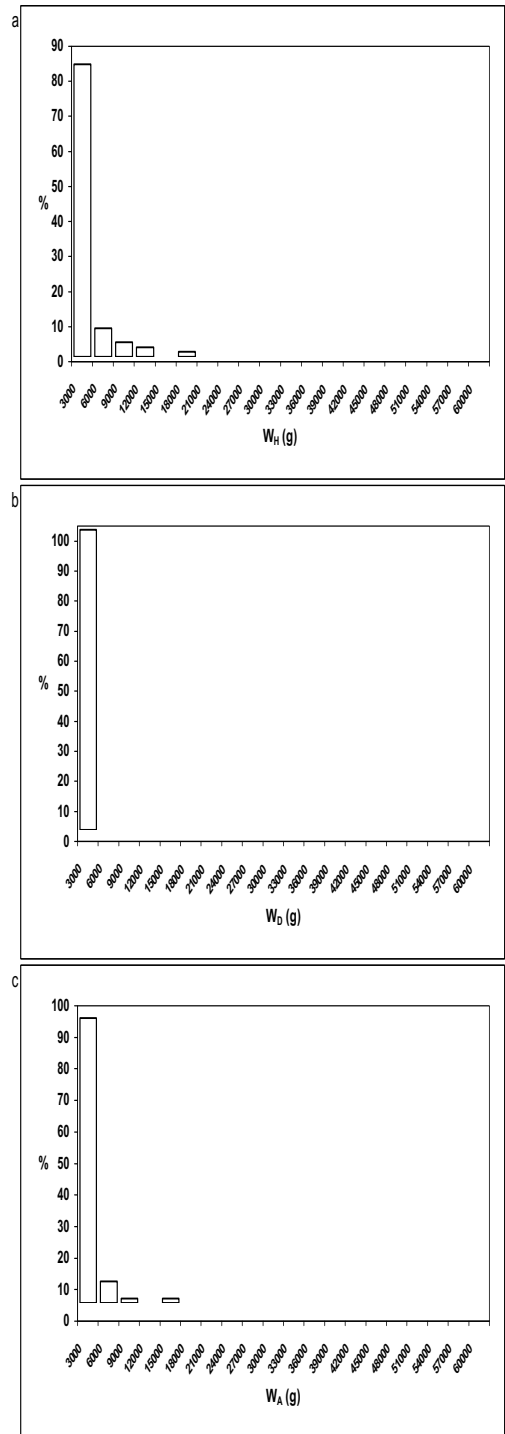


Fig. 7. Biomass-class frequency distributions for site 4 based on three different estimates of above-ground dry weight (a) W_H ; (b) W_D ; (c) W_A .

The population structures based on estimates of biomass are generally less variable than those based on measurements of plant size. While the size-class frequency distributions for sites 1-4 encompass each of the three general patterns outlined above, each of the frequency distributions based on estimates of biomass are of Type I (Figs 4-9). At least 40% of the plants at each site were estimated to be in the lowest biomass class and at site 4, estimates of biomass based on canopy diameter yielded a frequency histogram in which all plants were in that class. Most biomass-class distributions derived for sites 5 and 6 are less positively skewed than those for sites 1-4.

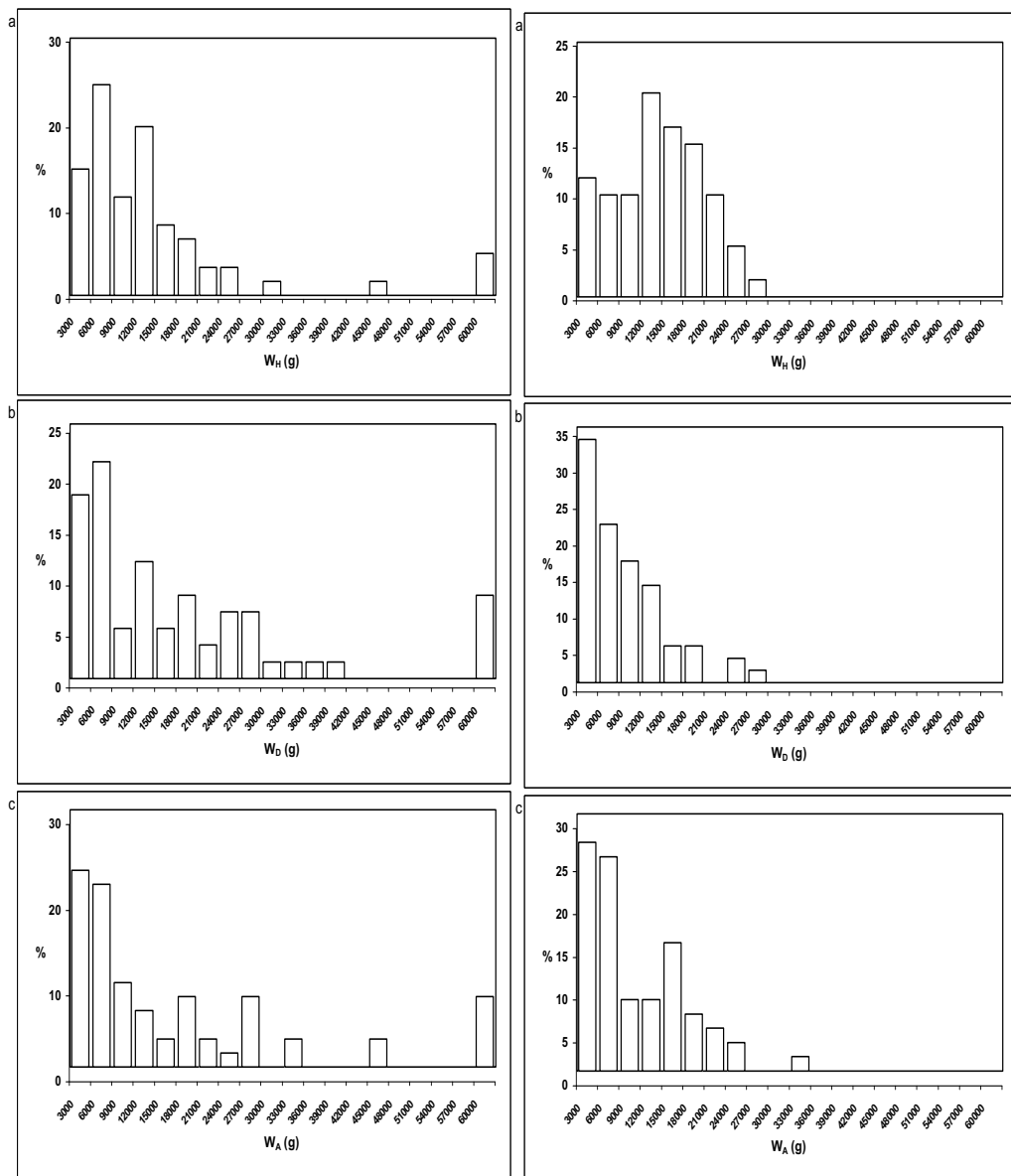


Fig. 8. Biomass-class frequency distributions for site 5 based on three different estimates of above-ground dry weight (a) W_H ; (b) W_D ; (c) W_A .

Fig. 9. Biomass-class frequency distributions for site 6 based on three different estimates of above-ground dry weight (a) W_H ; (b) W_D ; (c) W_A .

These data for *P. aculeata* indicate that plant population structures are strongly dependent upon the variables that are chosen to describe them. They also demonstrate that two variables can give rise to markedly different population structures even though there may be a strong correlation between the variables themselves. In *P. aculeata*, for example, 84% of the variation in canopy diameter can be accounted for in a linear relationship with plant height (Grice *et al.* 2002). However, size-class structures based on canopy diameter are more strongly positively skewed compared with the corresponding size-class structures based on height. This is simply because, especially in small plants, plant height tends to be greater than canopy diameter (Grice *et al.* 2002)

Importantly, the degree of skewedness in population structure data is very strongly influenced by the variable used. As illustrated by artificial data (Fig. 10), frequency distributions based on three-dimensional variables (e.g. volume, biomass) will be more strongly positively skewed compared with frequency distributions based on two-dimensional variables (e.g. projected canopy cover, stem cross-sectional area). Similarly, frequency distributions based on two-dimensional variables will be more strongly positively skewed compared with frequency distributions based on one-dimensional variables (e.g. height, canopy diameter, stem diameter). The skewedness is a function of plotting a non-linear variable on a linear scale, as happens in the analysis of plant size distributions.

Histories and projected futures of populations cannot be derived from descriptions of population structures unless there is additional information available. This must include at least general knowledge of the patterns of change in the size variables as the plant grows. To usefully compare population structures derived using different variables, it is necessary to know how those variables relate to one another. On the same grounds, it may be unreliable to draw comparisons between populations on the basis of similarities and differences between their population structures, even when those structures are based on the same variable. This is because growth patterns may differ between populations as a result of environmental or genetic variation amongst them.

Figure 10

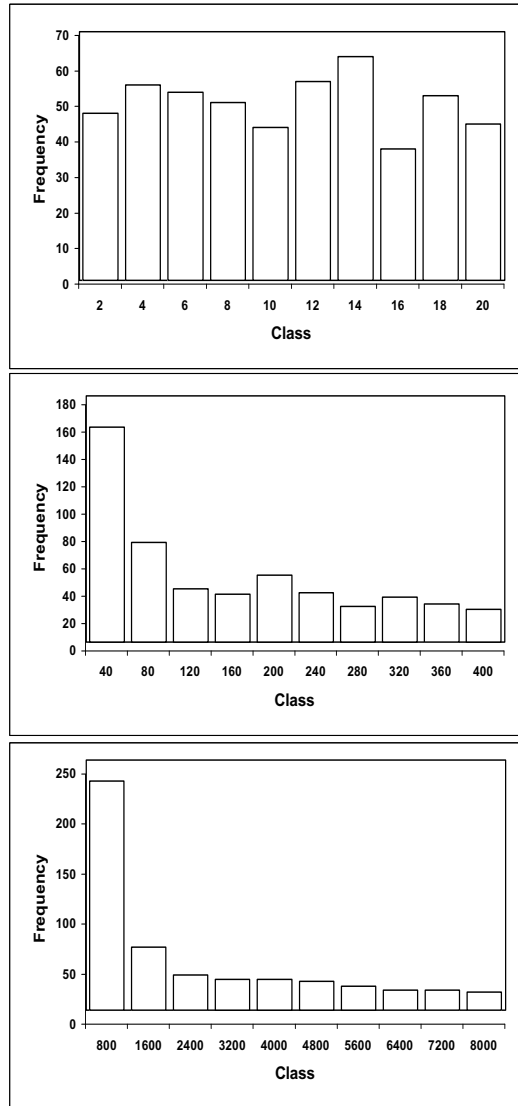


Fig. 10. Frequency distributions of (a) 500 random numbers ($0 < x < 20$); (b) the squares of the same 500 random numbers; (c) the cubes of the same 500 random numbers. In each case, values were assigned to ten evenly spaced class intervals.

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