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Original article

Development of *Cytisus scoparius* L. at stand and individual level in a mid-elevation mountain of the French Massif Central

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Abstract

Cytisus scoparius (L.) is a common native species of the Chaîne des Puys, a mid-elevation volcanic mountain range of the French Massif Central. Widely used in the former traditional agricultural system, broom has now become an invasive species colonising open areas after grazing abandonment. This study quantifies variation in size as a function of age and local competition at both stand and individual level. Eleven monospecific stands free of grazing were sampled according to an age gradient from young and recently established to old senescent populations. Density, age, mean dimensions and individual biomasses were measured. Intraspecific competition was assessed for 4–year-old broom plants by recording the number and size of neighboring broom within a fixed competitive radius. Age at which senescence occurred was also quantified. Results showed that the age distribution exhibited a clear peak in all stages, whereas diameter distribution shifted from a reversed J shape at the young stage to a broad range distribution at the terminal stage. Density decreased exponentially with time, while stand mean dimensions increased linearly for height, or followed a power model for stem diameter and crown width. On the individual scale, biomass was accurately predicted by stem diameter. Biomass, stem diameter and crown width increased with age without any asymptote, whereas height followed a sigmoid relation. However, at a given age, broom plant main dimensions were significantly reduced by competition that was quantified as the sum of the neighboring broom stem sections. The senescent terminal stage was characterized by a low density of individuals, a lack of seedling recruitment and age at senescence followed a normal distribution. Lastly, we replaced the above aerial development patterns by distinguishing three main stages of stand dynamics: stand initiation, stem exclusion and senescent stages.

Keywords: Cytisus scoparius; Growth; Competition; Age-class distribution

1. Introduction

European broom (*Cytisus scoparius* L.) is considered as an invasive species in many countries of the world because of its ability to colonize habitats where it has never previously occurred (Mack, 1985). Broom successfully invades a wide geographical range in New Zealand (Williams, 1981, 1983), USA (Bossard, 1991), Australia (Waterhouse, 1988) and India (Agrawal et al., 1961). The massive spread of this species is closely linked to specific traits of invasive species such as a production of high amounts of seeds forming a long lasting seed bank (Turner, 1933), a capacity to establish in areas immediately after a disturbance and fast initial growth (Fogarty and Facelli, 1999). Its tendency to form dense pure thickets in opened areas deeply alters the functioning of the ecosystem in place by modifying the environmental variables: light and soil moisture regimes and nitrogen dynamics (Diquélou and Rozé, 1999). Broom displaces the native ground vegetation and can therefore endanger the local biodiversity of the places it invades. It is also reputed to even prevent the recruitment of overstorey species (Smith and Harlen, 1991).

In France, especially in the mid-elevation mountains of the Massif Central, broom has not been considered a potential threat until recently because it is a native species and widely used in the traditional farming system. Broom was even a key component of agricultural activity in the 19th and up to the beginning of the 20th century. It was used to restore soil fertility and to produce firewood for bakeries (Rousseau

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and Loiseau, 1982; Bazin et al., 1983). Over recent decades the status of broom has changed because this species is no longer integrated in the currently more productive and specialized agricultural practices. It is now considered mostly as an invading species that preferentially colonizes abandoned pastures. As open areas are now less and less widespread due to land abandonment and forest colonization, these areas are considered of high interest for both their ecological and landscape values. Moreover, broom is also a nuisance for farmers because its extension decreases the value of pastures subjected to an extensive grazing regime.

Most studies on broom have focused on seed production and recruitment (see Paynter et al., 2000) because these aspects are of major importance in the case of invading species, but studies on growth and size development are less numerous (Fogarty and Facelli, 1999; Waloff and Richards, 1977). However growth related parameters are important in understanding how populations are organized and how they evolve through time. These parameters deeply influence the recruitment process because of interactions among these different biological components on an individual scale. They therefore play a role as important as the other biological attributes, especially in models simulating broom dynamics (Rees and Paynter, 1997) and incorporating spatial location and competition among individuals (Coquillard and Hill, 1997).

In this study we have focused on the development of aerial parts of broom within stands that have naturally established after grazing cessation. Our main goal was to investigate variation in size as a function of age and local competition. For a better understanding of stand development and individual variation the study was conducted at the population level and on an individual scale.

2. Material and methods

2.1. Sampling stands and aerial measurements

The study was conducted in a volcanic mid-elevation mountain range of the French Massif Central: la Chaîne des Puys (45°38′–45°55′ N and 2°47′–3°4′ E). This area is characterized by a mountainous climate: mean rainfall is 1000 mm equitably shared through the year and mean annual temperature is 7 °C at 900 m, the mean altitude of the region. The agricultural history of this area is marked by a sudden and large field abandonment after the second world war due to the collapse of the traditional farming system based on extensive sheep grazing. As a consequence natural afforestation occurred at a large scale.

The remaining pastures are now subjected to extensive and hazardous grazing and regularly colonized by broom shrubs that are then usually mechanically suppressed each 4–8 years. However many sites are periodically abandoned due to grazing decline and dense broom stands formed immediately after grazing withdrawing.

In such areas, we selected 11 monospecific stands of broom across an age gradient ranging from 1.3 to 6.4 years old. Stands were grouped according to their physiognomy and their mean age (Table 1). Sites were chosen in comparable sites free of any grazing and close to each other. In each stand one plot was assessed of a various size from 2 m^2 in dense and young stands up to 16 m^2 in old sparse stands. In each plot all individuals were counted, the diameter at the base of the shoot was measured with an electronic calliper (±0.01 mm) and age determined by ring counting on all individuals except for the most crowded plots in which a minimum of 30 individuals were measured. In addition, for a subset of 10–20 plants randomly chosen per plot, height and crown diameters in two perpendicular directions, were determined. A total of 36 plants were also sampled for biomass measurements. The woody part was separated from the green part (shoots of the 2 last years), dried at 80 °C for 3 days and weighed (±0.1 g).

In order to determine the longevity of broom, 63 dead plants were randomly sampled in senescent stands and their age determined by ring counting. These brooms were sampled only among the largest dead plants to avoid subdominant brooms that had died due to competition exerted by dominant plants. After smoothing, rings were also counted and measured for 14 individuals using Windro software (Regents Instruments, Québec).

2.2. Competition measurements

In order to identify the impact of intraspecific competition on above ground broom development, measurements were carried out within a 3–5 year old stand in the process of colonising an abandoned pasture. This age class was selected because it corresponded to a life stage in which competition is strong among growing broom plants. Several individuals subjected to different competition levels (i.e. different inten-

Table 1
Characteristics of the stands sampled along an age gradient and grouped in 4 stages. Mean and extreme values are indicated

Stages	Number of stands sampled	Plot size (m^2)	Age (year)	Density (/m^2)
Old senescent broom stand	3	9–12	6.3 (6.2–6.4)	2.9 (1.7–5.2)
Mature broom stand	3	8–16	4.7 (4.4–5.0)	8.7 (4.8–11.6)
Medium age broom stand	2	4–4.5	3.4 (3.3–3.5)	64.5 (62.3–67.6)
Young and dense broom stand	3	2.3–4	1.8 (1.3–2.0)	93.7 (58.8–125)

sity of local crowding) were selected in different parts of the stand, their position indicated and then cut to determine their age. As size is strongly related to age, it was important to measure competition effect on broom of similar ages. Therefore only 20, 4 year-old broom plants were selected, and measured (height, diameter at the shoot base and crown width), while the others were discarded from the study. Around each of these individuals (i.e. the subjects), the surrounding broom plants (i.e. the competitors) were counted and measured (height, diameter at the base) within a competition radius of 50 cm. The number of competitors ranged from 0 (isolated broom) to 63 (80 individuals/m^2). Lastly, all brooms (subjects and competitors) were removed, dried (80 °C, 3 days) and weighed.

2.3. Data analysis

Stand and individual models were derived using linear, power or exponential models. Dependent variables for stand models were stand density, mean height, mean crown width or mean diameter using mean age as the independent variable. Individual models were produced using age or diameter at stem base as independent variables.

Sigmoid models were developed using a regression equation derived from the Von Bertalanffy–Chapman-Richards growth model (Von Bertalanffy, 1968; Richards, 1959; Chapman, 1961) and computed as following:

$Y = A(1 - \exp(-bX))^c$

Where A is the asymptote value, b the rate parameter, c the shape parameter, X and Y are respectively the independent and dependent variables. Estimates were determined using an iterative search algorithm (Marquardt's method) that minimized the residual sum of squares. When not indicated, all P-values are <0.001. Analyses were performed using Statgraphics software (v. 5.1 Statistical Graphics Corp.)

3. Results

3.1. Stand structure and development

We have established the distribution in age and diameter classes of the different stands (Fig. 1) grouped according to their physiognomic description and age gradient (Table 1).

All stands are characterized by narrow age ranges and a dominant age class that forms a peak. As stands age it is possible to follow the translation of this peak from young to old age classes. It is also noteworthy that no young broom become established in the terminal stages. The distribution of individuals in diameter classes exhibit a different pattern. Young stands show a typical reversed J shape distribution indicating a gradual decrease in abundance from the lower to the higher diameter classes. For the following stages, a peak in the intermediate classes is visible but less pronounced in the medium and mature broom stands. In the oldest stands forming the final stage the distribution in diameter is characterized by a broad range and the absence of a clear dominant class.

Changes in the main stand variables with stand mean age are shown in Fig. 2. Density is maximum in younger stands which have just established, and reaches a value of more than 120 stems per m^2. Competition is maximal at this stage and is associated with large mortality rates. Consequently, density decreases rapidly following a negative exponential model. Older stands are the least crowded with a density of 1–5 stems per m^2. The drastic fall in density observed in growing stands is accompanied by an increase in mean dimensions of the individuals. Crown width and diameter at stem base can be accurately modelled by a power model whereas increase in height is almost constant among the different stages and follows a linear model.

3.2. Individual growth

Aerial development of broom was studied at the individual scale using the individuals sampled in the different

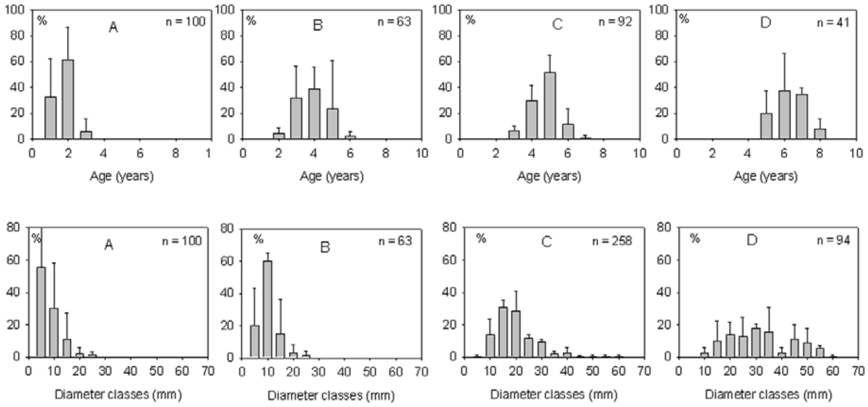

Fig. 1. Age and diameter class distributions of individuals through populations of various ages (mean value and standard deviation). n = number of individuals measured, A: young and dense stands, B: medium aged stands, C: mature stands, D: old and senescent stands. Diameter classes are defined each 5 mm.

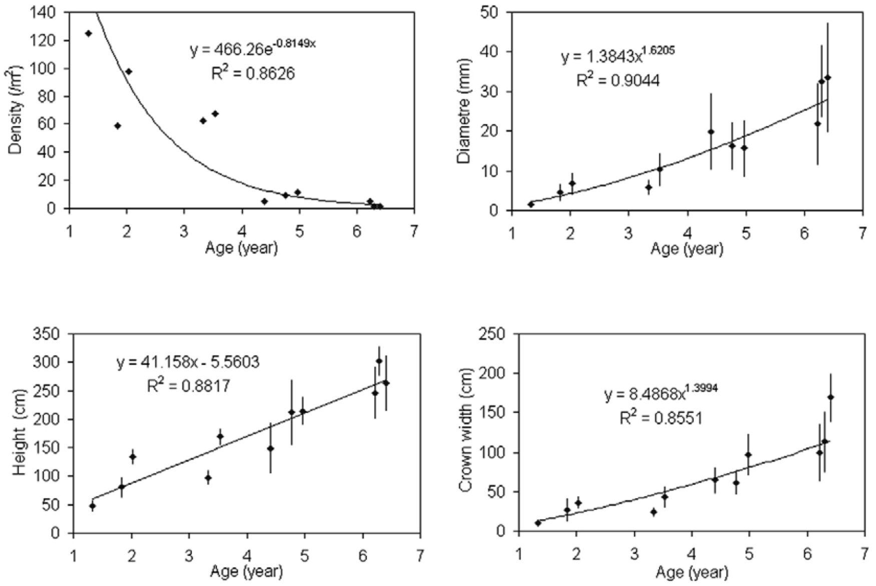

Fig. 2. Variation of stand density and individual dimensions (mean value and standard deviation) as function of stand age. Regressions are indicated.

stands. Radial growth measured on old broom plants within senescent stands increases with age up to a maximum of 3.3 mm per year at 5 years old (Fig. 3A), then ring width stabilizes. The absence of a clear and long decrease of ring width with age, commonly observed on most long-lived species like trees, appears to be a typical feature of broom which has been also reported for *Calluna vulgaris* (Coquillard et al., 2000). This explains why diameter increase with age does not show any slowdown (Fig. 3B) and can be described by a power instead of a classical sigmoid model.

Senescence begins early and occurs over a short period: at age of 7, most of the brooms are dead and the distribution of age at senescence follows a normal distribution (Fig. 4).

Also, crown width does not exhibit any stagnation in size while broom is ageing. Crown width is therefore very similar to diameter development (Fig. 5A) and these two variables prove to be very closely linked (Fig. 5B).

In contrast to diameter and crown width, height shows a different pattern. It appears that with increasing age, broom tends toward an asymptotic height value of 3.7 m in our study area (Fig. 6A). Height is also strongly linked with stem diameter but contrarily to crown size the relation is sigmoid (Fig. 6B). There is, therefore, a progressive stabilization of height whereas the stem diameter keeps increasing.

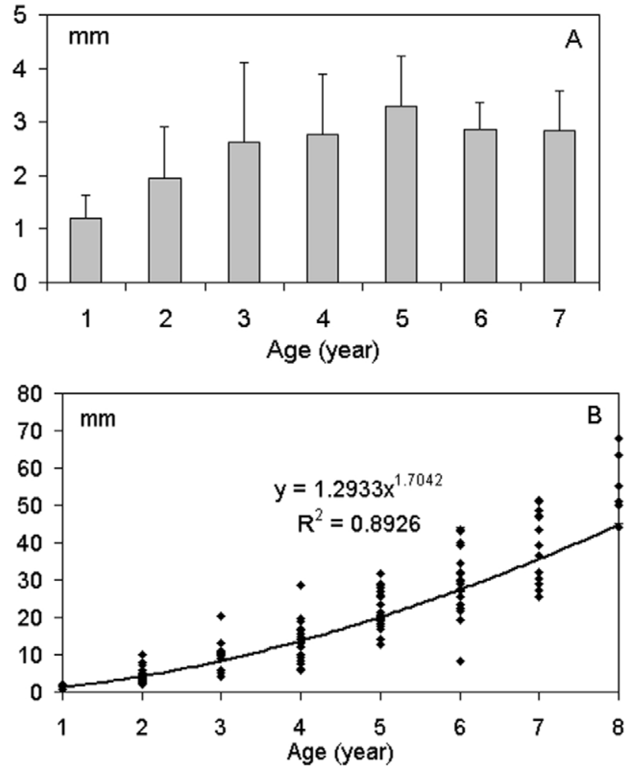

Fig. 3. Change in radial growth and diameter as function of age. (A) Radial growth (mean value and standard deviation) measured on 14 old brooms within stands, each bar represents the mean of a minimum of 9 radial growth measurements. (B) Diameter at the stem base as function of the individual age, regression curve is indicated.

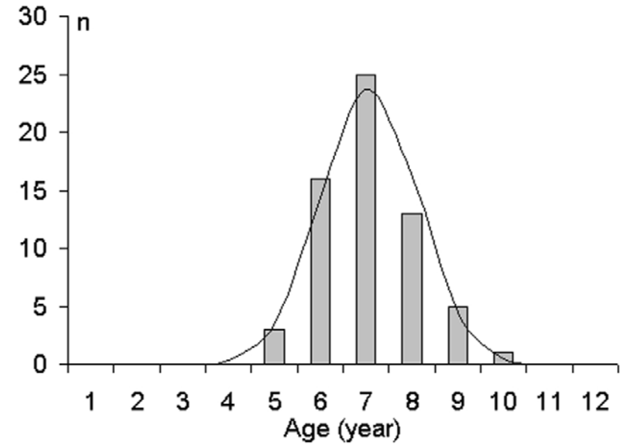

Fig. 4. Distribution of dead brooms (bars) and theoretical normal distribution (mean = 7.07, standard deviation = 1.06, χ^2 obs. = 0.88; $\chi^2_{0.05;1}$= 3.84; *P* = 0.35).

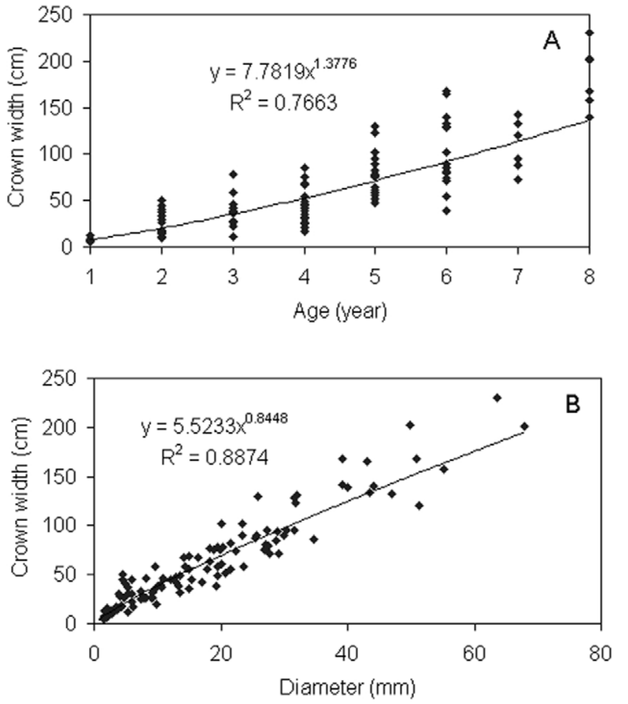

Fig. 5. Crown width as function of (A) age and (B) diameter at stem base for individuals within stands. Regressions are indicated.

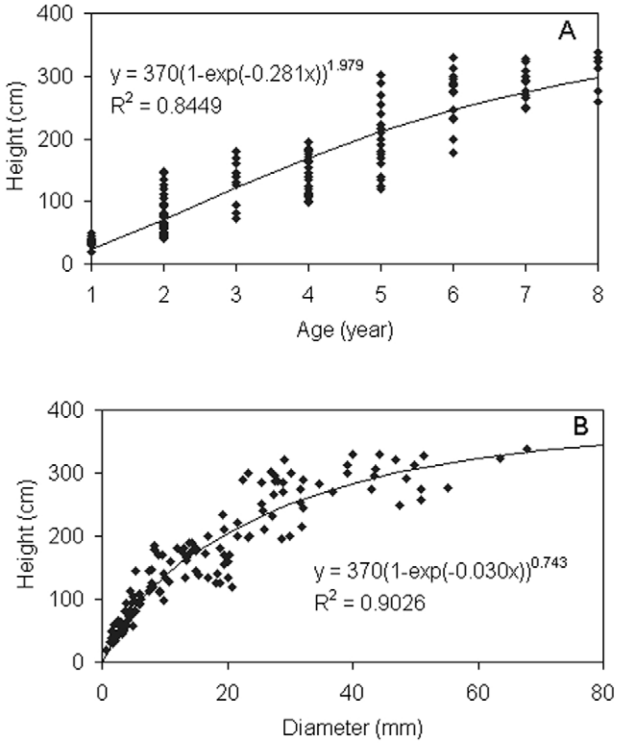

Fig. 6. Height as function of (A) Age and (B) Diameter at stem base for individuals within stands. Regressions are indicated.

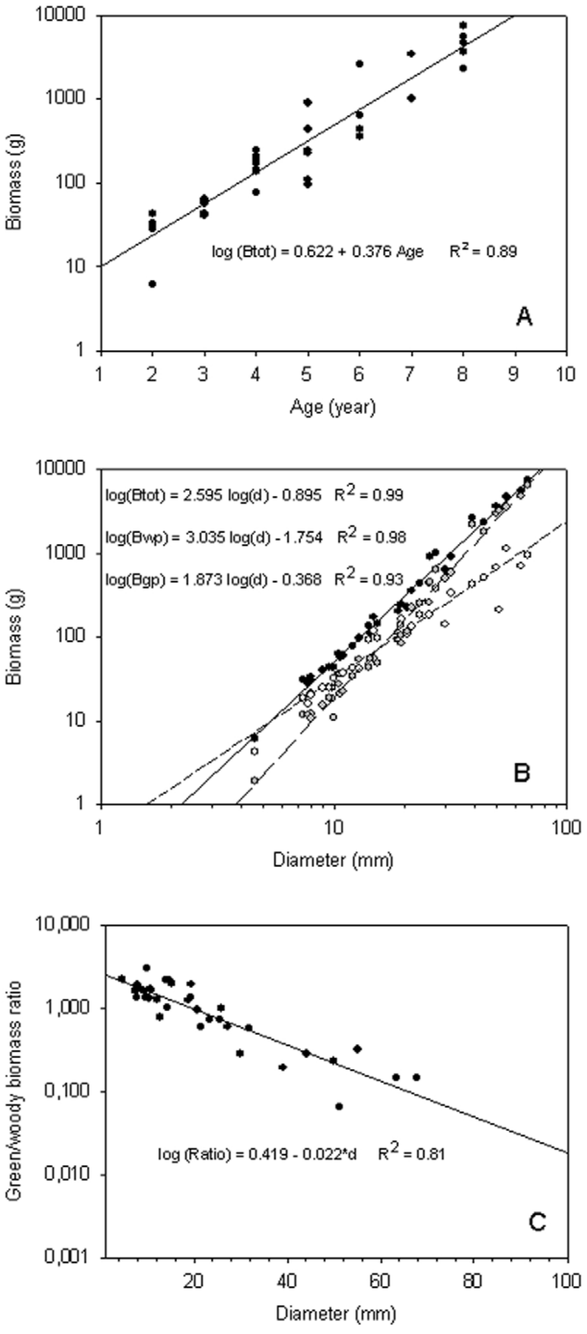

Fig. 7. (A) Biomass as function of age. (B) Biomass as function of diameter at stem base, $n = 36$, Btot: total biomass (black circles and solid line), Bwp: biomass of the woody parts (grey circles and long dash line), Bgp: biomass of the green parts (white circles and short dash line). (C) Green/woody biomass ratio as function of diameter at stem base. Regressions are indicated.

Individual broom biomass, like its other main dimensions, increases with age. However, this parameter does not exhibit any sign of slowdown with age (Fig. 7A). The best predictor of the individual biomass is the stem diameter (Fig. 7B) that proves to be a very integrative measure of the growth and competition conditions the individual has faced during its entire life. In a similar manner, the increase in 'green' biomass (i.e. photosynthetic biomass) and woody biomass is also closely related to diameter. The green biomass is dominant in broom of low diameter but quickly falls with increasing diameter, while the woody part gains dominance and, for mature subjects, the green: woody biomass ratio stabilizes around 2 (Fig. 7C).

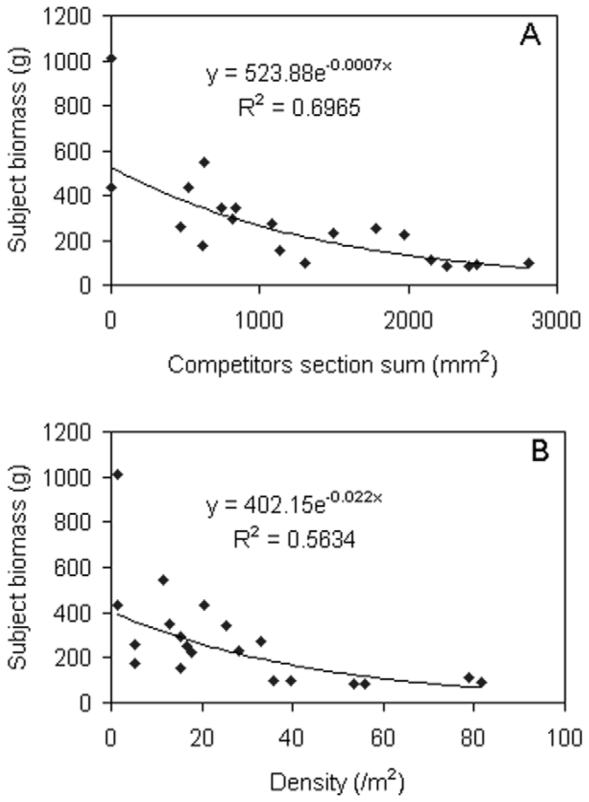

Fig. 8. Impact of intraspecific competition on the biomass of subject plants. Competition is measured as the sum of the section at stem base of neighboring brooms (A) or total density (B). Regressions are indicated.

3.3. Impact of intraspecific competition on individual growth

Biomasses of subject brooms of 4 years old were computed against two measurements of the local competition: sum of competitors' section and total density (Fig. 8). The development of above-ground parts of broom is negatively related to competition intensity: the greater the competition, the more reduced are the individual biomasses and stem diameters. Results show that density is a less accurate predictor than the sum of the competitors' sections. It is noteworthy that the total biomass of the competitors does not improve the relationship between biomass and competition (data not shown), as stem diameter is very strongly linked to total biomass.

Crown width is also reduced by competition, as measured as the sum of the competitors' sections, but less strongly ($R^2 = 0{,}472$, $P<0.001$) and height is not significantly related to competition ($P = 0.11$).

4. Discussion

Abandoned pastures of the Massif Central are often colonized by broom that can form dense and monospecific stands within the space of a few years. This ability of broom to establish rapidly is linked to massive (Waloff and Richards, 1977; Rees and Paynter, 1997) and early (Waloff and Richards, 1977; Paynter et al., 1998) production of seeds coupled with a long lasting seed bank, a seedling emergence and survival that is generally enhanced by soil disturbance (Paynter et al., 1998). Once established, stands evolve from dense and young to old and sparse, following a maturation process in which competition plays a major role. Similarly to other shrub or tree populations, it is possible to distinguish different stages in stand dynamics as proposed by Oliver and Larson (1996), in forest stand development.

4.1. Stand initiation stage

The stand initiation stage is the first and primordial stage in the course of which seedlings establish. Time as well as the intensity of this phase will determine the future structure of the stand. In our study brooms have rapidly invaded the available space in two or three years. Such a pattern can be explained by a major initial disturbance in abandoned pastures e.g. sudden withdrawal of the grazing regime that has produced a size-reduced vegetation and numerous gaps in which broom can settle. The use of mechanical methods (chopping, cutting, moving) to remove the ground vegetation in order to increase pasture value is also frequently practiced in the study area and such techniques can enhance broom invasion when it is followed by insufficient grazing pressure. Paynter et al. (1997) have emphasized the role of disturbance in broom establishment by bringing seeds close enough to the surface to germinate and by reducing competing vegetation. Similarly, Bossard (1991) found in California that germination did increase when soil was disturbed although Parker (2001) reported that removal of the cryptogam layer did not promote *Cytisus* establishment.

The fast establishment of broom has produced stands characterized by a narrow age class distribution, that was also reported in the same area by Rousseau and Loiseau (1982) in stands established on previous fallow communities. In contrast, these authors reported a more continuous and broader age distribution when brooms have developed on heathlands in which the vegetation in place was more competitive and offered less available sites for broom settlement.

4.2. Stem exclusion stage and impact of competition

When the available space is fully occupied, new individuals cannot appear because broom is largely unable to regenerate under its own canopy (Smith, 1994). Intraspecific competition among established broom plants is the main driving force that operates at the individual scale and deeply influences changes in stand structure. This process occurs in a stage called 'stem exclusion stage' in forest systems by Oliver and Larson (1996), it corresponds to our intermediate stages. This stage is characterized by an important increase in size at both stand and individual scales but also by a drastic reduction of the density. The diameter distribution shifts from a typical reversed J shape to a broader distribution in which peaks are less pronounced. Finally, this process seems to be similar to the 'self-thinning' phase of forest dynamics. In this study intraspecific competition is identified as the main cause of density decline because no visible impacts of natural broom enemies (invertebrate fauna) were found and decline due to meteorological factors, drought in particular, is unlikely on these well-watered and non-nutrient-limited soils. However, neither Paynter et al. (1998) nor Sheppard et al. (2002) found any evidence for density dependent mortality in broom stands although, as for this study, Paynter et al. (1998) noted increasing levels of intraspecific competition reduced plant growth. Direct manipulations of plant densities would probably give more conclusive evidence for intraspecific competition as the major cause of thinning.

Fast growth is another common feature of broom and of other invading shrub species in general, moreover its establishment is favoured in our area both by nutrient rich volcanic soils and a favourable climate. Fogarty and Facelli (1999) have also reported a high relative growth rate for broom in Australia that confers to this species an indubitable competitive advantage compared with other potential tree or shrub competitors. Fast growth leads to high competition that is of more importance in the case of nutrient-rich soils than in nutrient-poor soils because, according to Grime (1979), the ability to conserve resources in a stressful environment is just as important as their capture.

Growth and size development with age follow different models according to which plant parameters is taken into account. Crown (Fig. 5A) and stem diameter (Fig. 3B) are accurately fitted with a power model indicating that there is no obvious decrease in growth for these two dimensions until death occurs. Mortality has excluded numerous individuals and the remaining brooms are able to mobilize the newly available resources and thus increase their crown and stem dimensions. In contrast, height tends to stabilize with increasing age (Fig. 6A), a pattern that has been also reported by Waloff and Richards (1977). At a given age however, individual dimensions varied across a large range. Results have shown that the level of local competition at the individual scale can largely explain this variation in size (Fig. 8). Competition was assessed in this study with measurements based on local density (i.e. a measure of the number of competitors) and the sum of stem sections of neighboring brooms. These measures are also strongly related to the total competitors' biomass, as diameter is an accurate predictor of total biomass (Fig. 7). These competition measures are similar to competition indices used in forestry and belong to a set of non-spatialized indices (Tomé and Burkhart, 1989; Biging and Dobbertin, 1995; Prévosto et al., 2000). Such indices, which allow us to quantify directly competitive relationships in monospecific stands, are based on geometric measurements of competitors within a competition radius. Past studies have shown that an increasing competitive radius improved the relation between the competition value and size or growth of the subject but that benefits could be negligible beyond a certain distance (Pukkala and Kolström, 1987), mainly because competition is a localized process. Competition acts as a reductor of growth, especially on stem diameter and total biomass but less on height, although past studies have shown also a significant effect of interspecific competition on seedling height (Paynter et al., 1998). Consequently, in monospecific stands and at comparable age, stem diameter is a good descriptor of the local competition: the thinner the stem diameter, the more intense the local competition and vice versa. However, the maximum competition pressure the plant can face before dying still needs to be established in the context of producing mortality models.

4.3. Senescent stage

The senescent stage is composed of stands in which symptoms of decline such as the appearance of dead branches and twigs are visible. This process is not preceded by any obvious decrease in growth, just stagnation in ring width increments and in total height can be noticed. Senescence, therefore, appears as an autogenic process in the absence of major disturbances such as fire, storms or insect attacks that is mainly driven by age. In our dense monospecific stands average death occurs at 7.07 years and no broom older than 10 years was recorded. Short life spans were also reported by Waloff and Richards (1977) with an average life expectancy of 10–12 years in the United Kingdom. Rees and Paynter (1998) noted an average death of 10.2 years for a population in a forest clearing in the UK, and of 7.9 years in the French Pyrenees. Rousseau and Loiseau (1982) have found a comparable average life span to ours in the same area for a dense stand, but they also reported that, in a less crowded stand established on previous heathlands, brooms could live up to 12 years. It is noticeable that outside Europe life expectancy of broom is far greater, and can reach 17 years in USA (Bossard and Rejmanek, 1994) and more than 23 years in Australia (Smith and Harlen, 1991; Smith, 1994). These latter results suggest that the average life span is influenced by numerous factors such as environmental conditions, competition and also predation by insects (Waloff and Richards, 1977).

At this senescent stage, and contrary to earlier stages, a broad range in diameter distributions is observed (cf. Fig. 1). This results from the fact that broom plants still alive have faced a large range of competition conditions during their life and, as a consequence, a great variability in size is found. However, no young broom plants were encountered beneath the canopy of the old senescent individuals, though light has become much more available at this stage. This finding can be explained by the presence of a developed ground vegetation in which perennial grasses, herbs and semi-ligneous species are abundant (e.g. *Rubus* sp.). The competition exerted by this dense vegetation for both above and below-ground resources prevents broom seedlings from becoming successfully established as they are poor competitors (Paynter et al., 1998). Broom cannot therefore form permanent and stable stands and, in the absence of any new disturbance, natural succession involving this species in this area is largely unidirectional.

4.4. Invasiveness of broom

Within its native range in France, *Cytisus scoparius* has caused various problems in open habitats but the invasiveness of broom is by far less marked than within its exotic range. In particular it does not persist under forest cover and seems to be more closely related to pastures. The question is to understand why this species is such an invasive weed in areas where it is not native. Numerous hypotheses have been proposed to explain exotic plants invasiveness. One of the most widespread is the enemy release hypothesis arguing that the introduced organisms spread rapidly because they are liberated from attack by their natural enemies (Williamson, 1996; Van der Putten, 2002). Indeed, recent studies have supported this hypothesis by showing that fewer pathogens infect plant species in their naturalized range than in their native range (e.g. Mitchell and Power, 2003). It has been confirmed, in a study quantifying the invertebrate fauna on broom, that the average abundance of specialist phytophages is significantly higher in alien than in native habitats (Memmott et al., 2000). Herbivory leads to decreased growth rates, decreased recruitment and increased mortality on broom (Waloff and Richards, 1977). Therefore, such a difference in herbivory pattern can explain the weedy nature of this plant in exotic habitats (Memmott et al., 2000). However other mechanisms can also be put forward to explain broom invasiveness out of its native range. In particular, this study indicates a lack of seedling recruitment beneath broom stands in central France. Although it has to be confirmed by further studies in other sites, broom stands, in the absence of disturbance, are naturally replaced by other vegetation composed of semi-ligneous and ligneous species. As for this study, Paynter et al. (1998) have emphasized in southern France the failure of broom seedlings to establish beneath mature stands. By contrast, Sheppard et al. (2002) noted that seedling regeneration did occur under mature broom in exotic habitats and that there was only weak suppression of regeneration from the ground flora. This, combined with the spatial models of Rees and Paynter (1997) indicates a major difference in the persistence of broom stands between native and exotic habitats, which could explain why broom is such an invasive exotic weed. Moreover numerous factors such as fire, drought, browsing, grazing and density-dependence also influence scrub encroachment as demonstrated by Roques et al (2001) for a native legume shrub in Swaziland.

In conclusion, this study has brought us information and data on how broom populations are organized and how they develop. However, the better understanding of growth at population and individual scales holds theoretical and practical problems. Predicting the spread of invasive species requires knowledge on growth, recruitment, competition and mortality processes. Understanding how these processes occur at the individual scale and what are the main tradeoffs among them is of particular interest for insights into the overall population dynamics. Quantitative field data on broom aerial development can help elucidate patterns of variation in population growth and demographic rates. Such data are also widely used in invasive models of broom both by demographic models (Parker, 2000) or by spatially explicit models that incorporate local competitive interactions between individuals (Rees and Paynter, 1997).

From a practical point of view, little is known of the fluctuations of population demography and variation in growth of invasive species populations and how they have an impact on the composition of the host community that is colonized and changed through time. Better knowledge of these parameters could benefit the early detection and control of broom invasions (Carey, 1996; Parker, 2000).

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