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## The ecology of vulpia

**P.M. Dowling**, Co-operative Research Centre for Weed Management Systems, NSW Agriculture, Agricultural Research and Veterinary Centre, Orange, New South Wales 2800, Australia.

### Introduction

*Vulpia* (*Vulpia* spp.) comprises 20–28 species which occur in 4–5 sections (Cotton and Stace 1977, Ainscough *et al.* 1986), but rank status is extremely subjective. Four of the sections have some similarities to the genus *Festuca*, with section *Loretia* being most similar, while section *Vulpia* is most different. The other sections (*Spirachne*, *Apachloa* and *Monachne*) have characteristics lying between sections *Loretia* and *Vulpia* (Ainscough *et al.* 1986). These authors suggest the evolutionary trend appears to be from section *Loretia* (chasmogamous, perennial habit) to section *Vulpia* (cleistogamous, annual habit). Based on morphological and protein characters, taxa within section *Vulpia* are closely related and could be considered the one species (Bulinska-Radomska and Lester 1986).

The closeness of the genera is demonstrated by the existence of hybrids (*F. rubra* × *V. bromoides* (L.) Gray, *V. myuros* (L.) C.C. Gmel., *V. fasciculata* (Forssk.) Gray), with most reported confirmations occurring in the United Kingdom (Stace and Al-Bermani 1989) and the fact that in the United States of America, *V. myuros* is frequently referred to as *Festuca megalura* (Slayback 1985). Most of the species occurring in Australia belong to section *Vulpia* (*V. bromoides*, *V. myuros* (*V. megalura*), *V. ciliata*, *V. muralis*), while *V. fasciculata* belongs to section *Monachne*. *V. bromoides* and *V. myuros* are the two most common species in Australia and typically co-occur over a wide range of southern Australia (McIntyre and Whalley 1990), though they are more dominant on lighter, more acid soils (Rossiter 1966). Common names for individual species ('fescues') are confusing (Kloot and Symon 1982), especially when these species co-occur. Because of their prominence, further discussion will be limited to these two species and will be referred to collectively as vulpia.

### Distribution of *V. bromoides*, *V. myuros*

Surveys in eastern Australia indicate that *V. bromoides* occurs more frequently than *V. myuros* (>70% – Dellow and Dowling 1987, 61% vs. 38% – McIntyre and Whalley 1990, 75% vs. 24% – Leys and Dowling 1992, 70% vs. 30% – Jones 1992). These findings are contrary to previous studies in southern Australia reported by Dillon and Forcella (1984). In certain circumstances, each species appears to have a

preference for particular soil (*V. myuros* – basaltic soils, sheep camps (McIntyre and Whalley 1990)), and environmental conditions (on Tenerife, *V. bromoides* – common at low/moderate altitudes, *V. myuros* – widespread and common at moderate/high altitudes (Dickson *et al.* 1987), in Corsica, *V. myuros* – dry environments, steep slopes and acid/neutral soils (Volaire *et al.* 1991), in Spain, *V. bromoides* – drier Mediterranean regions (Vacher 1984, cited by Volaire *et al.* 1991)).

*Vulpia* follows the general life cycle of winter annuals and this has been defined by Bartolome (1976 – cited by Bartolome 1979):

- i. autumn germination of seeds produced mostly in the previous spring,
- ii. seedling establishment,
- iii. slow vegetative growth over autumn and winter,
- iv. flowering and seed production followed by senescence,
- v. summer carry-over of seed.

These stages provide a useful framework for reviewing the ecology of vulpia. Early research has been reviewed previously (Rossiter 1966). Most emphasis in this review however, is based on more recent studies.

### Autumn germination of seeds

This phase is governed by the timing and extent of the autumn rains, and the conditions prevailing at the seed-soil interface. Under Australian field conditions, vulpia matures over the period October–December, but before germination can occur, a period of after-ripening is required. In the glasshouse, this can be as long as 4–5 months, but in the field, shortened to 2–3 months (Dillon and Forcella 1984), or less. *Vulpia* germination occurs over a wide range of temperatures and this range increases with time and when germinated in light (Dillon and Forcella 1984). Effectively this means that germination can occur in any season. Optimum temperatures for germination were higher for *V. myuros* compared with *V. bromoides*, while *V. myuros* germinated faster in the dark. Jones (1992) also found that the germination rate of *V. myuros* was more rapid than *V. bromoides* but after 20 days, cumulative percentages were similar (>95%).

### Seedling establishment

The superior germination response by *V. myuros* was not reflected in field

emergence data (Jones 1992) which showed that its cumulative emergence over seven months was approximately half that of *V. bromoides* (21% vs. 46%). Dillon and Forcella (1984) demonstrated that *V. myuros* was able to emerge from greater sowing depths despite its comparatively smaller seed size (0.49 mg vs. 0.59 mg). This suggests that in a conventionally cultivated seedbed, the main vulpia species present would be *V. myuros*. However, emergence by both species was severely reduced at depths greater than 1 cm (Dillon and Forcella 1984). Vulpia then, is not expected to be a major weed problem in fully prepared seedbeds. Seed size though varies considerably (e.g. 0.35 mg – Dowling and Nicol 1993, 1.43 mg – Peart 1989b). The preference for germinating in light might explain the depressive effect of litter (4 t ha<sup>-1</sup> DM) in autumn where emergence of vulpia was reduced by ~70% (Jones 1992), though *V. bromoides* was not as severely affected by increase in DM.

Field emergence mainly occurs over the mid-winter period (McGowan 1970, Forcella 1984), though Jones (1992) found establishment occurred over nine months (January–September). Where vulpia is dominant, vulpia recruitment is related to level of seed production, but recruitment is low where perennials are dominant (Peart 1989a). Under coastal Californian conditions, a continuous seed rain is necessary to maintain a vulpia population in a perennial pasture, but the population is invariably low (Peart 1989b). It was also found that vegetation biomass, irrespective of species, was the best predictor of vulpia inhibition. Typical field populations of vulpia range from 4800 m<sup>-2</sup> (Dowling and Nicol 1993) to 43 000 m<sup>-2</sup> (Scott and Blair 1987) in moister tableland conditions, and lower in drier environments (Leys and Dowling 1992). Vulpia seedling number is a critical measurement since it is a major determinant of pasture composition in late winter (Arnold and Anderson 1987).

#### Vegetative growth

Dry matter production early in the growing season when temperatures are relatively high and photoperiods long, increases linearly, whereas later in the season when temperatures and photoperiods are lower and shorter, dry matter production is maximized by exponential growth (Dillon and Forcella 1984). Cumulative field dry matter production in monoculture was greater for *V. myuros* and with a March sowing, was as high as 10 t ha<sup>-1</sup> (Leys and Dowling 1992). Most of this production however, occurs in spring when quality feed is plentiful. Vulpia has a low phosphorus requirement (Loneragan and Asher 1967) and shows a limited response to increasing levels of phosphorus (at least

up to 125 kg ha<sup>-1</sup> superphosphate) in terms of dry matter production (Rossiter 1966). However, other annual species are more responsive to phosphorus (Ozanne *et al.* 1969) which could result in a lowered proportion of vulpia in the sward (Rossiter 1966). Vulpia appears to be able to absorb phosphorus more effectively at low soil values, and produce maximum yield at these low phosphate levels (Asher and Loneragan 1967). These and more recent studies (e.g. Dowling *et al.* 1996) suggest that reduction in per cent vulpia in the pasture by application of phosphorus is only likely to be marginally successful. Indeed, a survey of pastures where vulpia was present, revealed no relationship between incidence of vulpia and soil phosphate and soil pH (Leys and Dowling 1992). Vulpia incidence was lower where perennial grasses and annual grasses were present.

Vulpia has a high root:shoot ratio (Rossiter 1966) which means that it is vulnerable to sudden onset of dry conditions. However, because it flowers early relative to other annual grasses (Madin 1986), it can successfully avoid drying soils in late spring. The high proportion of roots in the surface soil (Joffre *et al.* 1987) suggests that competitive effects may involve nutrients rather than moisture, especially in pasture situations where phosphorus (low solubility in soil) is mostly broadcast onto the soil surface.

Higher levels of soil nitrogen tend to decrease the proportion of vulpia (= *Festuca megalura*) in an annual pasture (Evans 1960). Similarly, nitrogen was shown to decrease other vulpia parameters (Arnold and Anderson 1987). Vulpia had a lower dry matter response to nitrogen when compared with other annual grasses, but at typical field densities, the response was comparable (Cocks 1974), indicating that in a mixed grass sward, application of nitrogen is unlikely to result in lower percentage of vulpia as a result of competition.

#### Flowering and seed production

Conditions required for floral initiation varies for both species (Dillon and Forcella 1984). Floral initiation in *V. myuros* depends on short photoperiods and low temperatures, whereas *V. bromoides* is less demanding in its requirements, showing little vernalization response and relative insensitivity to photoperiod (Flood and Halloran 1982). These responses probably account for the restriction of vulpia to southern Australia and may help to explain the apparent dominance of *V. bromoides* in mixed populations.

Time of establishment has a large influence on seed production. Jones (1992) showed that vulpia plants establishing in March produced 53 times as many seeds as plants establishing in July, whereas in central and southern New South Wales,

the difference between April and June sowings was 2.5× (Leys and Dowling 1992). Vulpia density dependence is probably expressed more in terms of plant size and panicle and spikelet number m<sup>-2</sup> than in mortality (Watkinson and Harper 1978). Leys and Dowling (1992) showed that while *V. bromoides* produced more panicles m<sup>-2</sup> and *V. myuros* more spikelets panicle<sup>-1</sup>, florets per spikelet were similar for both species. In that experiment, *V. myuros* produced more seed, but it was evident that each species had different strategies for maximizing seed production.

Ecotypic variation within each species for heading and maturation dates differed widely (over 40 days), but heading was 10 days later for *V. myuros* (Leys and Dowling 1992). Variation is due to the diverse environments from which the ecotypes were collected. With the likelihood that in any one location, there will be a mixture of ecotypes and species, control measures dependent on timing will always be difficult.

#### Summer carry-over of seed

Vulpia produces large quantities of seed as would be expected with small seeded species, and typically produce more seed than necessary to maintain plant populations. A mixed pasture with 13% vulpia in autumn produced 265 000 seeds m<sup>-2</sup>, from which 4800 seedlings emerged in watered soil cores (Dowling and Nicol 1993). Though actual field emergence would be less (39% attrition rate – Arnold and Anderson 1987), there is still a large proportion of seeds/seedlings unaccounted for. Californian studies indicate that seed predation of *V. bromoides* is limited to 7% (Peart 1989a) in an ungrazed pasture. Other sources of seed loss have been attributed to grazing sheep (43% – Arnold and Anderson 1987, Dowling and Nicol 1993) or weathering (Dowling *et al.* 1996).

The reduction in emergence caused by high levels of dry matter (Jones 1992) means that these 'dormant' seeds are carried over for germination the following autumn. Vulpia was previously considered to have a short-lived seed bank and therefore unlikely to be a problem in cultivated seed beds (Dillon and Forcella 1984). However, under northern tablelands conditions, the seed bank can persist for three years (Jones 1992). Degree of dormancy is of the order *Lolium rigidum* Gaudin (annual ryegrass) > vulpia > *Bromus mollis* L. (soft brome) = *Hordeum* sp. (barley grass) (McGowan 1970), and extent appears to depend on the amount of litter present over autumn/winter – closely grazed 1%; lightly grazed 7% (Jones 1992); ungrazed pasture <3% – Peart 1989a). This level of dormancy could result in a return to original densities in 1–2 years (Jones 1992).

## Conclusions

*Vulpia* persistence in annual and perennial pastures is dependent on high seed production, dormancy allowing carryover of seed, and resistance to grazing of reproductive structures (e.g. low feed quality, barbed awns). Satisfactory management of *vulpia* in pastures will revolve around significantly reducing the seed load and minimizing dormancy. Based on results presented here, these aims might be achieved by reducing seed production (cultural, chemical, grazing in spring), maximizing seed weathering/predation over summer (grazing), minimizing seed dormancy (reducing litter in autumn) and maximizing interspecific competition (perennial pasture – high levels of ground cover and biomass; annual pasture – presence of other vigorously growing annual grasses).

## Questions for future research

- Why are perennial pastures in southern Australia unable to resist invasion by *vulpia*? Is grazing a factor?
- Population dynamics in mixed pastures – what are the other species doing and under what circumstances?
- Importance of the *bromoides/myruos* complex – does the ratio change; under what conditions does it change; is it important; can it be exploited?
- Ecotypic and specific composition of typical swards – would this information help our understanding?
- Subtle differences in climatic/soil requirements between species – can differences be exploited?
- What is the origin of the dormant population? – e.g. time of recruitment, microsite variation?
- How can possible management strategies be integrated?

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