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Performance of *Festuca arundinacea* Schreb. (Poaceae) populations in England

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ABSTRACT

The native grass *Festuca arundinacea* Schreb. is widespread in grasslands across the United Kingdom, and is considered to be highly variable and represented by a number of strains and ecotypes. A field survey of 151 individuals from 16 populations in England in which eight morphological traits, canopy cover, and the number of vegetative and flowering tillers was measured confirmed this variability. Principal Components Analysis showed a strong principal gradient of variability reflecting a continuum of mean individual size among populations. Among-population variability in size exceeded within-population variability supporting the view of extreme variability in native habitats. Populations in the most productive habitats had the largest individuals (e.g., mesotrophic grasslands and roadside verges with >100 vegetative tillers and >40 flowering tillers per individual) while stressful habitats supported relatively small individuals (for example an individual growing in coastal strand with eleven vegetative and three flowering tillers). There was no evidence of geographic structuring of populations with respect to morphological variability or any relationship to associate species composition among sites. Detrended Correspondence Analysis of associate species abundance indicated three types of community reflecting coastal, inland, and limestone substrate sites. Fungal endophyte infection was uncorrelated with plant size, but was significantly related to the plant communities in which *F. arundinacea* populations occurred. Inland populations had low endophyte infection frequencies (five of six < 20%), whereas coastal populations and populations growing over limestone often had 100% of individuals endophyte infected.

KEYWORDS: endophytes, morphological measurement, ordination, phenotypic variation, tall fescue.

INTRODUCTION

The grass *Festuca arundinacea* Schreb. is native to Great Britain and Europe (Gibson & Newman 2001). It is also cultivated worldwide as a forage and turf grass (Sleper & West 1996). In the United States alone some 14 million ha of *F. arundinacea* have been planted. In Great Britain, *F. arundinacea* is widespread, occurring as a component of 19 National Vegetation Classification (NVC) communities ranging between mesotrophic and calcareous grasslands, mires and swamps, and maritime communities, as well as weedy open habitats (Gibson & Newman 2001). Taxonomic descriptions of *F. arundinacea* describe the grass as being variable with different strains occupying distinct habitats (Hubbard 1984). Whilst there are a number of published reviews of the species (e.g. Sleper & West 1996), including a recent Biological Flora account (Gibson & Newman 2001), an account quantifying morphological variation among and within native habitats is not available. To date, studies have concentrated on ecotypic variation in morphology expressed in common-garden experiments (Chatterjee 1961; Robson 1968; Grynia 1980; Ueyama *et al.* 1992; Ueyama & Sato 1994). Other studies have concentrated on physiological comparisons among ecotypes of *F. arundinacea* (e.g., Stoddart 1995) and its agronomic importance (Buckner & Bush 1979).

Members of the grass family frequently exhibit substantial morphological variation that can be an expression of phenotypic plasticity or ecotypic variation. Much of this variation, including the potential range of phenotypic plasticity, is genetically based reflecting relatively high levels of genetic diversity and divergence among grass populations compared with other plant groups (Godt & Hamrick 1998). Grime *et al*. (1986) suggest that plants from highly productive habitats will exhibit higher morphological plasticity than plants of the same species from unproductive habitats.

Although genetic diversity levels in some populations of *F. arundinacea* are known (e.g. Sugiyama *et al*. 1980; Ceccarelli *et al*. 1992), the relationship to morphological diversity in native habitats is poorly understood (Ueyama & Sato 1994). Morphological development of *F. arundinacea* plants is likely to reflect the response of different genotypes to local environmental conditions (Sugiyama 1995), especially soil moisture (Grynia 1980). Indeed, Trist (1991) suggested that *F. arundinacea* var. *stricta* (Hack.) K. Richt was, in fact, an environmentally-induced variant and not a genetically distinct variety.

The objective of this study was to quantify the level of morphological variability of *F. arundinacea* within and among populations from sites representing a wide variety of native habitats across southern England. In view of the known ecotypic variation in *Festuca arundinacea* and its widespread distribution in many habitats, we hypothesised the occurrence of habitat-related morphological variation in this species. In common with other grasses (Godt & Hamrick 1998), we expected within-population variation to exceed among-population variation.

MATERIALS AND METHODS

FIELD WORK

Native populations from England were surveyed in June and July, 1999. Sites were chosen to represent the diversity of vegetation types in which *F. arundinacea* occurs naturally (Table 1). The sites were unimproved and ungrazed except by rabbits, and by sheep at Bolton Le Sands. The site at Cressbrook Dale was formerly stock-grazed. A number of the sites are mown at least once seasonally (Bibury Verges, Little Dartmouth 1, Drayton, Paiges Meadow, Wineham Lane, and probably Polegate Trail). Eight to ten individuals were randomly selected at each of the 16 sites. Morphological measurements were made upon each selected individual. These were (1) the number of flowering and vegetative stems per individual, (2) the length and width of the longest leaf on 5–8 vegetative tillers, and (3) on five reproductive tillers, the length of the flowering panicle, length and width of the uppermost culm leaf, culm height, and number of spikelets per panicle. Gregariousness was estimated for each individual on a 1 to 5 scale reflecting plants growing in a turf (1) to compact clumps (5). The canopy cover over bare ground of *F. arundinacea*, other grasses, herbs, and woody plants were estimated in a 0·75 m^2 circular quadrat centred around each individual. The abundance of associated species including *F. arundinacea* across each site were estimated using the DAFOR scale (D = dominant, A = abundant, F = frequent, O = occasional, and R = rare). The species abundance data were used to assign each site to a National Vegetation Classification (NVC) community type (Rodwell 1991a, b, 1992, 1995, 2000). Leaf sheath samples were collected and preserved in alcohol for later investigation of fungal endophyte status and are reported elsewhere (Spyreas *et al*. 2001a). Voucher specimens of a representative plant of *F. arundinacea* from each site are deposited in the herbarium at Southern Illinois University Carbondale. Nomenclature follows Stace (1997).

DATA ANALYSIS

Principal Components Analysis (PCA) was used to summarize variation of individuals within and among populations. The PCA was based upon the correlation matrix from values of ten morphological variables from 151 individuals sampled at 15 of the 16 sites (the Salisbury Plain site was excluded because of incomplete data). Significance of PCA components and loadings on significant components were tested using parallel analysis (Franklin *et al*. 1995). Correlations between independent variables, the PCA components, and DCA axes (see below) were tested using Spearman’s Rank correlation incorporating a Bonferroni adjustment to avoid Type I errors. The first component of an initial PCA (referred to hereafter as PCA_1) was strongly related to plant size (see results). Subsequent components were non-significant and uninformative because of this overriding size effect. To explore further variation among individuals, the value for each morphological variable was regressed against the PCA_1 first component scores (all regressions were significant at $P < 0{\cdot}05$). The correlation matrix of the residuals from these regressions were used in a second PCA (i.e., PCA_2). PCA_2 was thus based upon data in which the strong size effect had been removed.

Within- and among-population variability was assessed by comparing variance component estimates with separate one-way ANOVAs of morphological variables and the PCA_1 and PCA_2 component scores. In this analysis, the site in which a population occurred was treated as a random effect. With one treatment (i.e. site), two variance components were estimated, site and residual variance, with the former providing an estimate of among-population variability and the latter (technically the variance of the site means), estimating within-population variability.

Analyses were conducted using SAS-PC Ver 8·0 and JMP Ver 4.0.2 running under Windows 2000.

The relationship between sites based upon the abundance of *F. arundinacea* and associated species was assessed using Detrended Correspondence Analysis using PC-ORD (McCune & Mefford 1999). Species occurring at fewer than two sites were excluded from the analysis leaving a matrix of 79 species. The option to downweight rare species was employed. The correlation between DCA axes and morphological variables associated with *F. arundinacea* from each site, PCA component scores, and associated species diversity was tested using Spearman Rank correlation at a Bonferoni adjusted significance level.

Geographic substructing of the populations based upon associate species abundance and morphological variation of *F. arundinacea* was evaluted by calculating Mantel z-test statistics (in PC-ORD, McCune & Mefford 1999) between Sorenson's Distances among sites for the species abundance or morphological character matrices, and a matrix of inter-site geographic distances.

RESULTS

MORPHOLOGICAL VARIABILITY

Morphological data from the 16 populations are shown in Table 2. Individuals of *F. arundinacea* ranged in size from a plant with only two tillers growing in an arable field margin (Wytham; mean of 5·8 tillers per plant) to a plant with 386 tillers growing on waste ground alongside a footpath (Polegate; mean of 194 tillers per plant). Similarly, the mean height of flowering tillers ranged from 62 cm at coastal strand (Mill Bay) to 1·6 m in individuals at a disused rail track (Harrington) (the tallest flowering tiller was 2·3 m, also at this site).

Fecundity was calculated as the product of flowering tiller number times mean number of spikelets per panicle, and ranged from a mean of 37 spikelets per plant in the field margin at Wytham to 5,779 spikelets per plant at Berrow saltmarsh. Across all sites, the plant with lowest fecundity had 25 spikelets (Wytham), compared with the largest value (16,466 spikelets at Berrow). Fecundity was highly correlated with the morphological variables (all $P < 0{\cdot}0001$), and also with *F. arundinacea* cover ($r = 0{\cdot}50$, $df = 141$, $P < 0{\cdot}0001$), and cover of herbs and woody plants ($r = 0{\cdot}21$ and $0{\cdot}33$, $P = 0{\cdot}01$ and $P < 0{\cdot}0001$, respectively). Fecundity was negatively correlated with cover of grass and bare ground ($r = -0{\cdot}44$ and $-0{\cdot}30$, $P < 0{\cdot}0001$ and $P = 0{\cdot}0003$, respectively).

The morphological variables, including fecundity, were highly correlated with each other (Spearman's Rank correlation, all $P \ll 0{\cdot}05$) indicating that the largest plants not only had larger leaves, more vegetative tillers and taller flowering stems, but had more flowering stems with more spikelets.

PCA_1 extracted one significant component (eigenvalue = 5·30, variance accounted for = 53%); other components were not significant according to cut offs for eigenvalues established using parallel analysis. The first component of PCA_1 had high positive loadings for all of the morphological variables (significantly so for leaf length, culm leaf length, height, panicle length and spikelet number), reflecting the high correlation among the morphological variables. The component scores were subsequently used as an integrated measure of plant size allowing a ranking of populations (Fig. 1). There was a continuum in size from one population to another.

TABLE 1. CANOPY COVER OF PLANTS, NUMBER OF SPECIES, NVC VEGETATION TYPE, AND DOMINANT SPECIES AT SITES IN WHICH *F. ARUNDINACEA* WAS SURVEYED (SEE FOOTNOTE FOR LOCATIONS). THE CHALK GRASSLAND (A CG3 DOMINATED BY *BROMOPSIS ERECTA*) SHOWN IN TABLE 2 IS NOT INCLUDED BECAUSE OF INCOMPLETE DATA

	Habitat				
Variable	Arable field hedgerow[1]	Arable field margin[2]	Carboniferous limestone grassland[3]	Cliff-top grassland 1[4]	Cliff-top grassland 2[5]
Canopy cover (%)*					
F. arundinacea	33·8	5·0	9·0	14·5	6·0
Herbs	2·8	3·1	**	50·5	27·8
Other grasses	63·1	85·9	82·0	31·0	52·0
Woody plants	0·4	0	8·5	16·0	31·5
Bare ground	0	6·8	0·5	0	1·5
Total cover	100·1	94·0	95·5	112·0	117·3
No. of species	16	10	21	16	24
Dominant species (plus other characteristic species)	*Dactylis glomerata*, *Holcus lanatus*	*Lolium perenne*, *Poa trivialis*	No dominant species. Abundant species included *Arrhenatherum elatius*	*Festuca arundinacea*, *Pteridium aquilinum*	*Festuca rubra* subsp. *rubra*, *Anthoxanthum odoratum*
N.V.C. vegetation type	MG1	MG7a	MG1e	MC9	MC9

	Habitat				
Variable	Hay meadow[6]	Roadside hedge[7]	Roadside verge 1[8]	Roadside verge 2[9]	Salt marsh 1[10]
Canopy cover (%)*					
F. arundinacea	26·5	22·5	35·0	45·9	60·6
Herbs	16·0	49·5	22·5	28·6	15·7
Other grasses	65·5	17·5	26	42·7	17·1
Woody plants	0·5	19	0	0	18·8
Bare ground	0·2	0	28	0·9	0
Total cover	108·5	108·5	83·5	117·2	112·2
No. of species	24	26	22	23	22
Dominant species (plus other characteristic species)	*Dactylis glomerata*, *Holcus lanatus*, *Rumex obtusifolius*	*Festuca arundinacea*, *Rubus fruticosus* agg.	*Arrhenatherum elatius*, *Heracleum sphondylium*	*Arrhenatherum elatius*, *Festuca arundinacea*	*Festuca rubra* subsp. *rubra*, *Phragmites australis*, *Rubus fruticosus* agg.
N.V.C. vegetation type	MG7b	MG1b	MG1b	MG1b	S26b/MG12b

TABLE 1. CONTINUED

	Habitat				
Variable	Salt marsh2[11]	Strandline 1[12]	Strandline 2[13]	Waste ground 1[14]	Waste ground 2[15]
Canopy cover (%)*					
F. arundinacea	11·0	13·5	16·5	41·5	46·0
Herbs	**	16·5	29·5	**	5·0
Other grasses	68·5	32	17·2	47·0	34·0
Woody plants	0	26	0·5	6·5	14·0
Bare ground	20·5	11·5	39·3	5·0	0·5
Total cover	78·5	88·0	63·7	94·5	99·0
No. of species	21	25	11	32	21
Dominant species (plus other characteristic species)	No dominant species. Abundant species included *Agrostis stolonifera, Festuca rubra,* subsp. *rubra, Glaux maritima* & *Trifolium repens*	*Carex pendula, Festuca arundinacea*	*Festuca rubra subsp. rubra, Lolium perenne* (with *Elytrigia juncea* ssp. *boreoatlantica*)	*Festuca arundinacea*	*Deschampsia caespitosa, Festuca arundinacea, Rubus fruticosus* agg.
N.V.C. vegetation type	MG12	W2	SD2/SD4	MG1	MG9b

* Estimated in 0·75 m^2 circular plots centered around each individual.

** Cover of herbs included in grass category.

Site locations: 1. Drayton, Warwickshire (SP165550), 2. Wytham Woods, Oxfordshire (SP461081), 3. Cressbrook Dale, Derbyshire (SK172744), 4. Little Dartmouth 3, Devon (SX874492), 5. Little Dartmouth 5, Devon (SX874492), 6. Paiges Meadow, West Sussex (TQ315245), 7. Little Dartmouth 1, Devon (SX874492), 8. Bibury Verges, Gloucestershire (SP119048), 9. Wineham Lane, Bolney, West Sussex (TQ238215), 10. Berrow Marsh, Somerset (ST290518), 11. Bolton-le-Sands, Lancashire (SD479693), 12. Fairlight Glen, East Sussex (TQ853107), 13. Mill Bay, Devon (SX742383), 14. Disused railway trackside, Harrington, Cumbria (NX998248), 15. Cuckoo Trail footpath, Polegate, East Sussex (TQ584056). Data for canopy cover and morphological data in Table 2 for Paiges Meadow, Polgate, Little Dartmouth 3, Wytham, Berrow, and Fairlight Glen were published previously in Gibson & Newman (2001).

TABLE 2. MEAN (± 1 SE) MORPHOLOGICAL MEASUREMENTS AND COUNTS FROM DIFFERENT HABITATS FOR *FESTUCA ARUNDINACEA*. THREE MEASUREMENTS WERE MADE ON EACH OF 10–12 PLANTS PER HABITAT

	Habitat			
Variable	Arable field hedgerow	Arable field margin	Carboniferous Limestone grassland	Chalk grassland†
Canopy cover (%)	33.8 ± 6·2	5·0 ± 0·0	9·0 ± 1·2	–
Panicle length (cm)	19·2 ± 0·9	14·0 ± 1·2	30·1 ± 1·4	25·6 ± 1·1
Spikelets per panicle	43·0 ± 6·2	30·6 ± 3·0	100·2 ± 8·7	95·2 ± 7·9
Leaf length (cm)	54·6 ± 2·1	26·9 ± 2·8	69·1 ± 3·2	35·3 ± 3·7
Leaf width (mm)	6·0 ± 0·3	4·3 ± 0·3	7·4 ± 0·3	3·9 ± 0·5
Upper culm leaf Length (cm)	11·7 ± 1·5	7·2 ± 1·2	15·7 ± 2·3	11·3 ± 3·6
Width (mm)	4·9 ± 0·5	3·9 ± 0·4	4·3 ± 0·4	4·0 ± 1·1
Culm height (cm)	117·7 ± 3·8	93·9 ± 4·2	155·2 ± 4·8	110·3 ± 5·5
Flowering/vegetative tillers per individual	5·5/30·6	1·3/4·5	5·5/13·1	9·4/11·8
Gregariousness*	4·3 ± 0·1	5·0 ± 0·0	3·7 ± 0·3	–

	Habitat			
Variable	Cliff-top grassland 1	Cliff-top grassland 2	Hay meadow	Roadside hedge
Canopy cover (%)	14·5 ± 1·4	6·0 ± 0·7	26·5 ± 5·1	22·5 ± 3·1
Panicle length (cm)	23·1 ± 1·5	22·3 ± 2·2	19·5 ± 1·7	32·4 ± 1·7
Spikelets per panicle	90·1 ± 9·4	79·8 ± 19·2	56·0 ± 7·3	133·9 ±9·7
Leaf length (cm)	53·5 ± 4·2	43·2 ± 3·0	38·5 ± 2·6	66·2 ± 3·8
Leaf width (mm)	6·3 ± 0·2	5·4 ± 0·4	6·0 ± 0·3	6·9 ± 0·4
Upper culm leaf Length (cm)	13·0 ± 1·8	14·2 ± 3·1	12·4 ± 1·5	23·7 ± 2·1
Width (mm)	5·0 ± 0·5	4·2 ± 0·5	5·4 ± 0·5	5·9 ± 0·5
Culm height (cm)	127·7 ± 4·9	109·7 ± 5·6	97·0 ± 6·3	139·1± 7·5
Flowering/vegetative tillers per individual	6·6/22·3	2·3/3·6	20·5/68·4	12·7/27·2
Gregariousness*	4·7 ± 0·2	5·0 ± 0·0	4·3 ± 0·3	5·0 ± 0·0

Some populations consisted of smaller individuals (low component scores) than in other populations (e.g., the saltmarsh population from Bolton-le-Sands compared with the populations at Berrow salt marsh and Polegate trail: see Fig. 1 and Table 2). The scores from this component were positively correlated with the canopy cover and fecundity of *F. arundinacea* (Spearman's r = 0·40 and 0·74, df = 139, P <0·0001, respectively), woody plant cover (r = 0·53, P <0·0001), and negatively correlated with the combined cover of herbs and other grasses (r = -0·31, P = 0·0002) and cover of bare ground (r = -0·47, P <0·0001).

To address Grime *et al.*'s (1986) hypothesis relating morphological plasticity to productivity, the regression was calculated between variance of PCA_1 component scores (as a measure of plasticity), and total plant cover per site (habitat productivity). Estimated in this manner, morphological plasticity was positively, albeit poorly related to productivity, when data from the Harrington site is excluded as an outlier (PCA_1 variance = -0·10 + 0·0035 (total cover), adjusted R^2 = 0·18, P = 0·07).

Three significant PCA_2 components were extracted, of which components 1 and 2 had significant loadings (eigenvalues = 2·57 and 2·03, variance accounted for = 26% and 20%, for components 1 and 2, respectively). There were no significant variable loadings on component 3, and it was not considered for further interpretation. Parallel analysis showed that Component 1 was significantly negatively related to the number of vegetative tillers, and positively related to panicle length. Component 2 was negatively related to the length and width of the youngest, fully expanded culm leaf. There was considerable overlap in the distribution of populations with respect

TABLE 2. CONTINUED

Variable		Habitat			
		Roadside verge 1	Roadside verge 2	Salt marsh 1	Salt marsh 2
Canopy cover (%)		35·0 ± 5·6	45·9 ± 5·3	60·6 ± 11·1	11·0 ± 2·2
Panicle length (cm)		20·5 ± 1·3	18·8 ± 1·1	30·9 ± 1·6	12·1 ± 0·9
Spikelet number		57·9 ± 7·4	41·6 ± 3·1	131·3 ± 14·2	39·6 ± 2·7
Leaf length (cm)		57·7 ± 6·5	34·6 ± 2·4	63·3 ± 6·7	23·8 ± 4·0
Leaf width (mm)		6·0 ± 0·4	4·8 ± 0·2	6·6 ± 0·3	3·7 ± 0·3
Upper culm leaf	Length (cm)	15·1 ± 1·4	10·2 ± 0·9	18·6 ± 1·7	4·6 ± 1·0
	Width (mm)	6·0 ± 0·3	4·0 ± 0·3	6·0 ± 0·4	1·8 ± 0·1
Culm height (cm)		119·9 ± 6·6	102·6 ± 7·4	147·8 ± 8·7	77·5 ± 6·4
Flowering/vegetative tillers per individual		2·6/44·6	4·1/8·3	31·9/172·2	8·1/10·3
Gregariousness*		2·9 ± 0·3	4·5 ± 0·2	4·8 ± 0·1	2·7 ± 0·3

Variable		Habitat			
		Strandline 1	Strandline 2	Waste ground 1	Waste ground 2
Canopy cover (%)		13·5 ± 5·7	16·5 ± 2·2	41·5 ± 4·6	46·0 ± 8·8
Panicle length (cm)		20·9 ± 1·8	17·2 ± 1·4	32·1 ± 2·3	27·2 ± 1·7
Spikelet number		68·2 ± 9·9	60·1 ± 5·9	139·0 ± 11·8	85·5 ± 14·7
Leaf length (cm)		29·2 ± 3·1	24·9 ± 2·4	74·5 ± 6·8	73.0 ± 4·9
Leaf width (mm)		5·7 ± 0·3	6·5 ± 0·3	9·4 ± 0·6	7·4 ± 0·3
Upper culm leaf	Length (cm)	8·1 ± 1·2	8·5 ± 1·3	13·3 ± 2·0	21·6 ± 1·5
	Width (mm)	2·6 ± 0·2	4·5 ± 0·4	4·5 ± 0·6	6·3 ± 0·5
Culm height (cm)		106·0 ± 10·0	61·5 ± 4·2	163·7 ± 9·6	151·6 ± 5·4
Flowering/vegetative tillers per individual		4·8/8·9	3·3/11·1	33·2/55·6	40·2/153·8
Gregariousness*		4·9 ± 0·1	4·4 ± 0·2	4·7 ± 0·1	4·7 ± 0·2

†CG3 Salisbury Plain, Wiltshire (ST918468).
*Estimated on a 1 to 5 scale reflecting plants growing as a turf (1) to highly clumped (5).

to components 1 and 2 (Fig. 2). Two of the northern populations, i.e., those from Harrington and Cressbrook Dale were relatively distinct from the other populations by having high component 1 and 2 values corresponding to low loadings for culm leaf length and width, and high loadings for panicle length. Some populations such as Mill Bay and Wineham Lane showed minimal variation with respect to the integrated response of these characters, whereas others such as Polegate and Berrow were highly variable. The first component of PCA$_2$ was positively correlated with canopy cover of herbs and other grasses (Spearman's r = 0·27, df = 141, P = 0·001), woody plant cover (r = 0·29, P = 0·0006), and the ratio of the number of flowering to vegetative tillers per individual (r = 0·30, P = 0·0003). It was negatively correlated with *F. arundinacea* canopy cover (r = -0·39, P <0·0001) and the total number of tillers per individual (r = 0·46, P <0·0001). The second component of PCA$_2$ was positively correlated with herb cover (r = 0·23, P = 0·006) and negatively correlated with other grass cover (r = -0·36, P <0·0001).

There was no significant correlation between species richness per site or endophyte infection levels, and the component scores for either PCA$_1$, PCA$_2$, or fecundity.

Among-population variability exceeded within-population variability for eight of the ten morphological variables. Among-population variability ranged 56–70 % of the total variance for these eight variables. The two variables in which within-population variability exceeded among-population variability were culm leaf length and width (among-population variance of 54 and 58%, respectively). Among-population variability of overall plant size (i.e., PCA$_1$ axis 1 scores) was 74% of total variance, exceeding within-population variance (Fig 3). When overall plant size reflected in PCA$_1$ was accounted for in the analysis (i.e., PCA$_2$), within-population variability exceeded among-population variability (within-population variance of 59 and 61% for PCA$_2$ components 1 and 2, respectively; Fig 3).

PLANT COMMUNITY RELATIONSHIPS

The 16 populations occurred in a wide range of habitats ranging from established grasslands (e.g., carboniferous limestone, cliff-top grassland, chalk grassland) and coastal habitats (e.g., saltmarshes and strandline) to disturbed habitats (e.g., roadside hedges and verges, arable field margins) (Table 1). Nine N.V.C. communities were represented, with mesotrophic grasslands (i.e., MG1, MG7, MG9, and MG12) being the most frequent. *Festuca arundinacea* ranged in abundance from occasional to dominant in these sites with a canopy cover ranging from nine to 61%. It was a dominant species at six sites including a cliff-top grassland, roadside hedge and verge, strandline and waste ground. Among the 16 sites, 201 associated vascular plant taxa were recorded. The most common associated species were grasses, notably *Festuca rubra* ssp. *rubra* (nine sites, dominant in three), *Dactylis glomerata* (14 sites, dominant in one), *Arrhenatherum elatius* (12 sites, dominant in two), *Holcus lanatus* (eleven sites, dominant in one), and *Agrostis stolonifera* (eleven sites, none dominant), plus the shrub *Rubus fruticosus* agg (eleven sites, none dominant), and herb *Plantago lanceolata* (eight sites, none dominant) were also common.

Two axes (eigenvalues of 0·43 and 0·27 for axes 1 and 2, respectively) were retained for interpretation following a Detrended Correspondence Analysis of associate species abundance. The distribution of sites with respect to these two axes allowed the discrimination of three main groups; two limestone-based sites, six inland sites, and eight coastal sites (Fig 4). A suite of species were limited in their distribution to the two limestone-based sites. These were *Anthyllis vulneraria, Carex flacca, Centaurea scabiosa, Filipendula vulgaris, Helianthemum nummularium, Linum catharticum, Polygala vulgaris, Primula veris, Sanguisorba minor, Scabiosa columbaria, Succisa pratensis, Trisetum flavescens*, and *Valeriana officinalis*. Other species with high abundance at these sites and also present elsewhere included *Briza media, Crataegus monogyna, Festuca ovina, Pimpinella saxifraga*, and *Viola hirta* (Pearson Correlation with DCA axis 1 all > 0·8, P « 0·01). Discrimination of associate species among the inland and coastal sites was less clear, but *Festuca rubra* was clearly associated with the coastal sites (Pearson Correlation with DCA axis 2 = 0·78, P <0·01), and *Dactylis glomerata* and *Poa trivialis* were associated with the inland sites (Pearson Correlation with DCA axis 2 = -0·71 and -0·75, respectively, P <0·01). To a lesser extent, *Agrostis capillaris, Cynosurus cristatus, Elytrigia repens, Holcus lanatus, Lolium perenne, Phleum pratense*, and *Ranunculus acris* were associated with the inland sites (Pearson Correlations all -0·5 to -0·7, P <0·01). *Festuca arundinacea* was not significantly correlated with either axis but was most adundant in the coastal and inland sites compared with the limestone-based sites. Widespread species such as *Rubus fruticosus* agg., and *Plantago lanceolata* were not particularly associated with any specific type of vegetation or the DCA axes.

The first DCA axis was correlated with endophyte infection frequency (Spearman’s r = 0·78, df = 14, p = 0·0009). Populations in which endophyte infection frequency was less than 60% were restricted to inland sites, all of which had low axis 1 and axis 2 values. No other variables, including those related to morphology of *F. arundinacea*, met the Bonferoni corrected level of significance (p = 0·0013 for a set of 38 correlations) for correlation with either DCA axis.

Mantel tests revealed no significant geographic substructuring of the populations based upon either the abundance of associate species or morphological variation in *F. arundinacea* (standardized Mantel statistics = 0·052 and 0·124 for associate species and morphological variables, respectively; P >0·05 in both cases).

DISCUSSION

The data presented here support the hypothesis for genotype x environment morphological variation in populations of *Festuca arundinacea.* Contrary to our expectations (Godt & Hamrick 1998), within-population variation was not greater than among-population variation, except after removal of a size effect).

Results confirm the extreme variability of *F. arundinacea* across native habitats in England. The habitats themselves were varied, ranging from field margins, beach fronts, and the margins of saltmarshes, to mesophytic and calcareous grassland. However, in no case was *F. arundinacea* observed directly under a woody canopy. The plant communities in which *Festuca arundinacea*

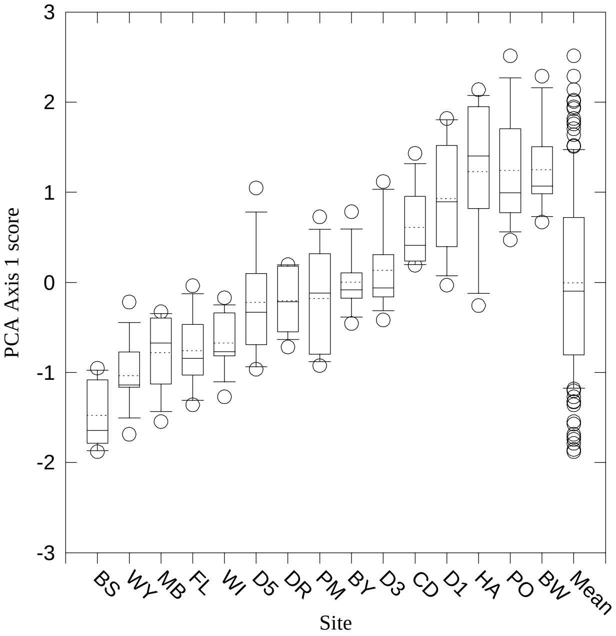

FIGURE 1. Tukey box plot of PCA_1 component one scores. Populations are ranked by mean (dashed line) score. BS = Bolton-le-Sands, Lancashire; BW = Berrow marsh, Somerset; BY = Bibury verges, Gloucestershire; CD = Cressbrook Dale, Derbyshire; D1 = Little Dartmouth hedge row, Devon; D3 = Little Dartmouth upper cliff, Devon; D5 = Little Dartmouth lower cliff, Devon; DR = Drayton, Warwickshire; FL = Fairlight Glen, East Sussex; HA = Harrington, Cumbria; MB = Mill Bay, Devon; PM = Paiges Meadow, West Sussex; PO = Polegate, East Sussex; WI = Wineham Lane, West Sussex; WY = Wytham Woods, Oxfordshire.

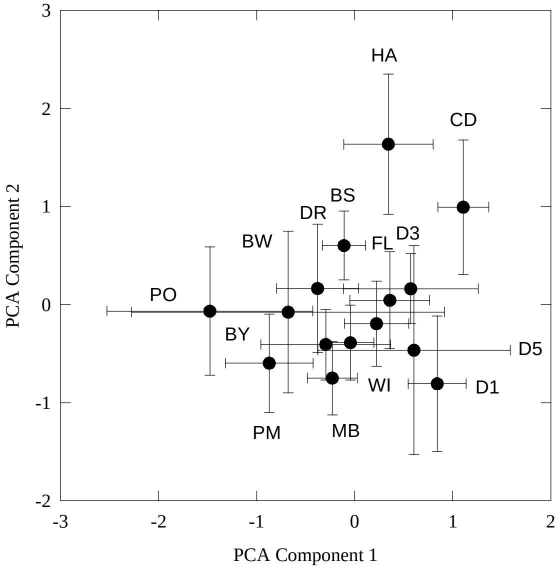

FIGURE 2. Principal components analysis (PCA_2) of 110 *Festuca arundinacea* individuals from 15 sites. The centroid of the location of individuals from each site is shown (solid circle) ± 1 SE bar. Sites identified according to codes in Figure 1. Component 1 was significantly negatively related to the number of vegetative tillers per individual and positively to panicle length. Component 2 was negatively related to length and width of the youngest, fully expanded culm leaf.

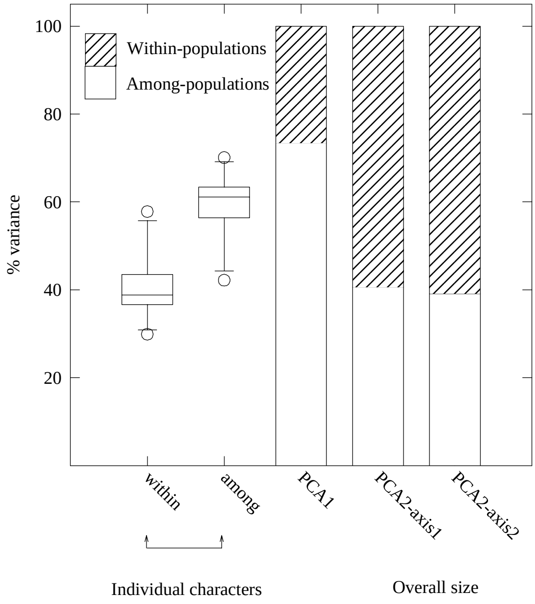

FIGURE 3. Variance components estimates for within- and among-population variability in *Festuca arundinacea*.

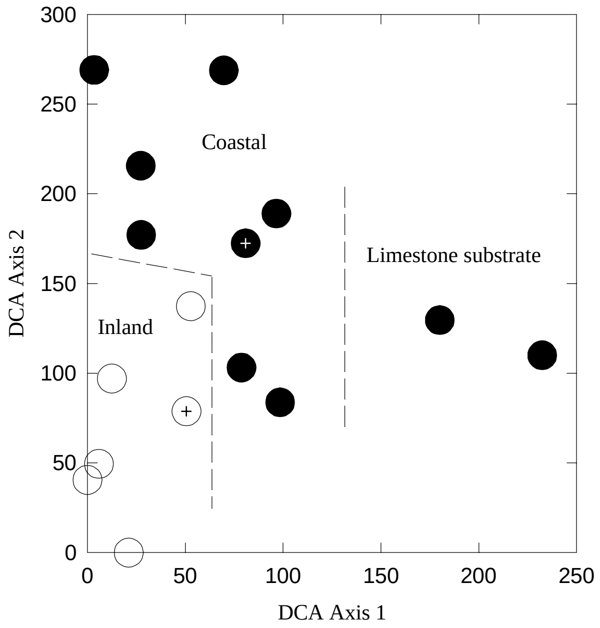

FIGURE 4. Detrended Correspondence Analysis (DCA) of associate species abundance from 16 sites in which *Festuca arundinacea* occurs. Symbols indicate endophyte infection frequency (from Spyreas *et al*. 2001a), filled symbols >85%, open symbols <20% except Polegate at 58%, '+' inside one of the indicates the Polegate site, and '+' inside one of the filled symbols indicates a site in which it was not possible to determine endophyte infection frequency.

populations were associated, fell into three general types; inland, coastal and limestone-based (Fig. 4) representing 10 NVC plant communities. It is noteworthy that we observed *F. arundinacea* to be particularly frequent in roadside MG1 communities, a vegetation type in which it has not been reported to occur previously (Rodwell 1992; Gibson & Newman 2001), despite its presence in this community in the N.V.C. database (A. J. C. Malloch, pers. comm.).

Within the habitats sampled here, *F. arundinacea* was often restricted in occurrence to a very narrow area. For example, at Berrow saltmarsh, it occurred only along the narrow (< 2 m wide) margin between the upper salt marsh and the old shoreline (Willis 1990). At the two beach habitats (Fairlight Glen and Mill Bay), the population occurred exclusively at the rear of the beach. At Bibury verges, *F. arundinacea* was restricted to within 1 m of the roadside. In other habitats, *F. arundinacea* was an important and widespread component of the grassland vegetation, e.g., cliff-top grasslands at Little Dartmouth, Paiges hay meadow, roadside verges at Wineham Lane and Little Dartmouth 1, calcareous grassland at Salisbury Plain and carboniferous limestone grassland at Cressbrook Dale.

The presence of fungal endophytes in *F. arundinacea* may be playing an important role in the population dynamics of this species (Clay 1998). Endophyte infection frequency of *F. arundinacea* was low or zero in the inland sites and high (> 85%) in the coastal and limestone-based sites (Fig. 3). It is possible that endophyte infected *F. arundinacea* populations at the inland sites have been out-competed by colonization from nearby pastures or roadsides sown with the endophyte-free S170 cultivar (Latch *et al*. 1987). Alternatively, the coastal and limestone habitats may be too stressful to allow endophyte-free populations of *F. arundinacea* to persist in competition with vigorous endophyte-infected individuals (Shelby & Dalrymple 1993). Fungal endophytes improve drought resistance in *F. arundinacea* (West 1994; Elbersen & West 1996; Hill *et al.* 1996) and may allow infected individuals to survive the moisture limited and saline conditions of coastal environments. The presence of endophyte infection has been shown to be affected by environmental factors and can lead to an increase in the proportion of infected individuals under moisture stress (Spyreas *et al*. 2001b). Furthermore, the presence of fungal endophytes in grasses, especially *F. arundinacea*, can have a significant negative affect upon associated species diversity (Clay 1997a, b; Clay & Holah 1999), although this relationship was not observed in this study.

The principal and overriding gradient in morphological variability corresponded to overall plant size. This observation is in contrast to Sugiyama *et al*.'s (1980) findings from a common-garden study of 19 ecotypes of *F. arundinacea* from European countries where two principal gradients of variability, also obtained using Principal Components Analysis, contrasted seed size/phenology with seasonal growth pattern. In their study, culm length and the number of florets per head were negatively correlated, whereas in our study these two variables, and all other morphological variables, were positively correlated. The place of origin of the plants in Sugiyama *et al*.'s (1980) study was more widespread than described here, and they included a Japanese and North American cultivar.

In this study, large plants, in all measured parameters, occurred in the most productive habitats. However, these habitats were compositionally quite varied; for example, the hedgerow at Little Dartmouth 1, the hiking trail at Polegate, the railway trackway at Harrington, and the Berrow salt marsh. The smallest plants were observed in unproductive and stressful habitats, such as beach strandlines (Mill Bay, Fairlight Glen), disturbed field margins (Wytham Woods) and Bolton-le-Sands saltmarsh. There are few other studies on *F. arundinacea* with which to compare these data. Nevertheless, the culm heights and panicle lengths observed in the present study were similar or somewhat larger than reported for Polish ecotypes (Grynia 1980), but smaller than reported for Moroccan plants (Ueyama & Sato 1994). Overall, the range of sizes found in this study is within those reported for the species (Hubbard 1984; Stace 1997). An exception was the length of vegetative leaves which Hubbard (1984) reports as ranging from 10 – 60 cm. Vegetative leaves > 60 cm were observed in this study at nine sites, with the population mean > 60 cm at the roadside hedge at Little Dartmouth, the salt marsh (Berrow), the trail (Polegate), railway trackside (Harrington) and the Carboniferous grassland (Cressbrook Dale). The maximum leaf length was 1050 cm measured on a plant growing in the roadside verge at Bibury.

Festuca arundinacea exhibits ecotypic variation across its natural range (Chatterjee 1961; Grynia 1980; Ueyama & Sato 1994). Hubbard (1984) suggests that different strains occupy distinct habitats with the largest individuals in the most productive habitats. Our study supports this observation. The largest plants were found at the four sites noted above where the mean vegetative leaf length exceed 60 cm. These were highly productive habitats, despite being very different vegetation types (S26c, MG9b, and MG1b NVC types, respectively: see Rodwell 1992; 1995). Similarly, the smallest plants were from the shorelines at Mill Bay and Fairlight Glen. These two sites were highly disturbed and the *F. arundinacea* populations occupied a narrow zone subject to high levels of salt spray. However, there was considerable overlap in plant size among the different populations (Fig. 1) that does not support the occurrence of discrete strains or ecotypes as suggested by Hubbard (1984). There was also a lack of any geographic structuring in the size of individuals among populations (Fig. 1) in contrast to observations of Polish plants (Grynia 1980) and of Sugiyama *et al.*'s (1980) study of ecotypes collected from sites in several European countries. For example, the Mill Bay and Fairlight Glen sites were the most geographically distant (>310 km apart), yet the plants from these sites were small and showed complete overlap in size (Fig. 1). Similarly, the plants from Polegate Trail and Berrow salt marsh were large, overlapped in size, but were separated by over 225 km. After accounting for plant size in the data analysis, there was considerable overlap in the extent of population variation (Fig. 2).

If ecotypes do exist across the range of populations studied in southern England, then there is considerable overlap with respect to the morphological variables measured in this study. This variability was reflected in the greater among- than within-population variability. A common-garden experiment or molecular analysis would be required to establish the occurrence of ecotypes among these populations (e.g., Dixon 2001) and determine the extent of the genotype by environment interaction. Much of the variation among populations is likely a phenotypic response to the local environment, which, itself is a product of genotypic variation (Cheplick 1991). Grime *et al.* (1986) have suggested that plants from highly productive habitats exhibit higher morphological plasticity than plants from unproductive habitats. Our data for *Festuca arundinacea* populations do not support this view with only a poor relationship between morphological variance and habitat productivity. We observed the largest, but not necessarily the most variable plants in the most productive habitats. Experiments with the S170 cultivar of *Festuca arundinacea* have shown that inflorescence characters, including seed number per panicle, are subject to both genetic and genetic by environmental control (Bean 1969).

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