University of Groningen

Do intrinsically dominant and subordinate species exist? A test statistic for field data

Oloff, Han; Bakker, Jan P.

Published in:
Applied Vegetation Science

DOI:
[10.2307/1479081](https://doi.org/10.2307/1479081)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1998

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Oloff, H., & Bakker, J. P. (1998). Do intrinsically dominant and subordinate species exist? A test statistic for field data. *Applied Vegetation Science*, 1(1), 15-20. <https://doi.org/10.2307/1479081>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Do intrinsically dominant and subordinate species exist? A test statistic for field data

Oloff, Han^{1*} & Bakker, Jan P.²

¹Nature Conservation and Plant Ecology Group, Department of Environmental Sciences, Wageningen Agricultural University, Bornsesteeg 69, 6708 PD Wageningen, The Netherlands;

²Laboratory of Plant Ecology, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands;

*Corresponding author; Fax +31 317 484845; E-mail han.olloff@ton.wau.nl

Abstract. We propose a new method to obtain information about processes that structure plant communities. We analysed the relationship between the presence and dominance of species across a range of habitats. A simple regression model was used to describe this relationship for each species. Based on the regression parameters, we distinguished *globally dominant* species, which dominate in the same proportion of plots within a habitat as in which they occur, *locally dominant* species, which reach dominance only when present in almost every plot of a habitat, and *intrinsically subordinate* species, which never attain dominance. We tested this method using a large data set of species occurrences across a range of salt marsh habitats. The relationships between presence and dominance could be described well by the regressions, and showed large differences between the species. Global dominants occurred later in the succession and higher on the elevational gradient than intrinsically subordinate species. Local dominants were characteristic of early successional stages. These patterns are discussed in the light of colonisation-competition and tolerance-competition trade-offs.

Keywords: Global dominant; Local dominant; Presence-dominance relationship; Regression model; Salt marsh; Succession.

Introduction

There is a long-standing dispute over whether the analysis of field data of species occurrences and co-occurrences can disclose the forces at work in structuring a community (e.g. Connor & Simberloff 1979; Fox 1987; Wilson 1989; Drake 1990; Stone & Roberts 1992; Goldberg 1995). Most studies trying to do this focus on the qualitative aspect of community composition, by investigating which species co-occur under certain conditions. Much fewer studies try to unravel why species differ in their relative abundances when co-occurring (but see Grime 1984). Interacting effects of plant traits and environmental factors determine the relative abundances of plant species within communities. Inherent adaptations of a plant population to specific environmental constraints often lead to reduced fitness under other con-

ditions, e.g., due to trade-offs between the investment of nutrients and energy in different plant parts or functions (Tilman 1990). Therefore, specific environmental conditions have their own characteristic dominants. Relatively unfavourable environmental conditions for a species can prevent a species from becoming one of the dominants, but it may still occur as a subordinate species. Species which are dominant under certain conditions may be subordinate in other, less favourable conditions. The reverse is, however, less clear. Whenever a species is found to be subordinate in a certain community, it is not *a priori* clear that it will be dominant somewhere else. Some species may just lack the traits needed to achieve dominance at all which would make them intrinsically subordinate species. It is important to identify these subordinate species, since they may be the first to become extinct if the habitat is perturbed. Intrinsically dominant species may be less vulnerable to extinction.

Large differences in niche width of plant species exist (Austin 1985, 1986), meaning that some species occur under a wide range of conditions, while others have narrower habitat requirements. Interspecific differences in phenotypic plasticity are especially thought to be responsible for this (Grime et al. 1986). More plastic species may be able to adapt to more different types of conditions, and hence achieve competitive superiority in many different habitats. Species lacking these features are expected to occur only under quite specific conditions in narrow 'windows of opportunities' as small-scale gaps, or only in a short period of the year (e.g. winter annuals).

A clear distinction between different dominance types may be useful with respect to conservation issues. Species that are subordinate throughout their whole distribution are expected to have small effective population sizes and may hence be more vulnerable to extinction due to environmental fluctuations (Rabinowitz 1981; Hodgson 1986). Those species may therefore be the first to which conservation measures, such as reintroduction, should be directed at.

Various terms and classifications have been used to distinguish between species differing in dominance characteristics. Species which are able to dominate under many different conditions have been termed dominants (Grime 1984), matrix species, competitors (Grime 1973) or core species (Wisheu & Keddy 1992) while species which rarely attain dominance have been called subordinate (Grime 1984), fugitive (Platt & Weiss 1985), satellite (Wisheu & Keddy 1992), interstitial (Keddy et al. 1994) or redundant (Rastetter & Shaver 1996) species. Although many authors distinguish between dominance types of species, we lack clear criteria to distinguish between them. We are not even certain whether such distinctions are ecologically valid. Just to observe that a species occurs in high abundance over large areas would not be enough to identify it as an intrinsically dominant species. The conditions under which it attains dominance may be quite unique, but homogeneous over a large geographic range. A species which occurs somewhere at low dominance may, or may not, be a dominant somewhere else (Rabinowitz 1981). Across-habitat studies should therefore be performed to solve this problem.

In this study we develop a method to classify species into different dominance types using field data of species occurrences in a range of habitats. This may contribute to the understanding of the ecological processes that determine community structure and species richness.

A new method

A habitat, i.e. a homogeneous area covered by a certain vegetation type, can be considered as a grid with small-scale, plots – say 1 m² – each of which can contain a certain number of species. An intrinsically dominant species which has colonized a certain proportion of the plots of a certain habitat is expected to dominate in the same proportion of plots of that habitat. Dominance is defined here as having the highest, second highest or third highest cover in the plot under consideration. If that species in another habitat occupies even more plots, it will also be a dominant species in more plots. For intrinsically subordinate species this relation is expected to be different. In general, the relationship between presence and dominance of species in communities may take three different forms:

1. A species becomes one of the dominants in the same proportion of plots in which it occurs in a habitat (*global dominants*). The fraction of plots in which a species is one of the dominants increases proportionally with the fraction of plots in which a species is present

2. A species becomes one of the dominants only if it occurs in most plots in a habitat (*local dominants*). The fraction of plots in which a species is one of the domi-

nants increases exponentially with the fraction of plots in which a species is present

3. A species never attains dominance, not even when found in most of the plots of a habitat (*subordinates*).

We tried to distinguish between these three cases by first grouping vegetation samples into a range of habitat types based on environmental characteristics, and then studying the relationship across habitats between the proportion of plots in which a species occurs (p) and the proportion of plots in which a species is one of the dominants (d). An arbitrary cut-off level for performance is needed to identify a species as a dominant. Dependence of d on p can be explored by fitting a simple power function to across-habitat data:

$$d = Lp^G \quad (1)$$

where parameter L indicates the proportion of plots in which the species is dominant at complete presence ($p=1$), and the parameter G indicates the relative rate at which d increases with p towards L .

When G approaches 1, this means that a species is dominant in the same proportion of plots in which it is present, and L is expected to be 1 (Fig. 1). This would make this species a global dominant. When the value of L is still high (between 0.5 and 1) but G is much higher than 1, then the species increases in dominance at higher presence, which makes it a local dominant (Fig. 1). When L is much lower than 1 and G is equal or lower than 1, the species is a subordinate species (Fig. 1).

Test of the method on salt marsh vegetation

The method was tested using data collected in a previous study on zonation and succession in a coastal salt marsh on the Dutch island of Schiermonnikoog. A full account of the layout of the study plots and ecology of the area is given by Olff et al. (1997). In this study, transects from higher dune foots to the low salt marsh were studied in a chronosequence of ages ranging from 10, 25, 35, 60 and 100 yr of vegetation and soil development since bare sand flats. The progress of succession was determined from aerial photographs. Succession proceeds in this system by accumulation of silt due to sedimentation, especially towards the lower end of the gradient. The lower salt marsh is inundated more often, and is therefore more saline and waterlogged. In each of the five areas with estimated successional age, we placed a grid consisting of 11 vertical and a variable number of horizontal rows of 1 m² plots (51–60, depending on the local topography) located adjacent to each other in a grid. For every 1-m² plot we measured elevation (m) with respect to Mean High Tide (MHT, 0.95 m above

Fig. 1. Identification of three types of dominance in ecological communities, as determined by the dependence of the proportional dominance (d) of a species on the proportional presence (p) across a range of habitats. Each line represents an example of a species with a different presence-dominance relationship, with the parameters of the regression model $d = L p^G$ (see Eq. 1).

Dutch Ordnance Level) using a theodolite. During June and July 1991 we determined for each of the 3927 plots which species were present, and which three 'dominant' species had the highest percentage cover (determined subjectively). The other species were considered subordinate. For the distinction of habitats, we divided the elevation gradient in each of the transects in three classes: 1: $< 0.45 \text{ m} + \text{MHT}$; 2: $0.45 - 0.65 \text{ m} + \text{MHT}$; 3: $> 0.65 \text{ m N.A.P.}$

The combination of three elevational classes and five successional ages provided 15 habitats, for which the proportion of plots occupied and the proportion in which a species was dominant, was calculated. In total, 36 species were found reflecting the species-poor nature of these salt marsh communities, of which only 13 species occurred in 15% or more of the plots. For these species, we studied the dependence of proportional occupancy

and proportional dominance across habitats ($n=15$). Eq. 1 was fitted to the data of these species using non-linear regression (Levenberg-Marquardt algorithm), which allowed the inclusion of zero percent dominance data at a certain proportional presence (a species can be present in a certain proportion of the plots within a habitat without ever attaining dominance).

In order to explore if the resulting parameters for each species reflected something about the ecology of the species we related these parameters to the successional position of the species and their position along the elevational gradient. The successional position was calculated as the weighted average of the years in which the species occurred. The elevational position was calculated as the weighted average of all elevations at which a species occurred. This method resembles the calculation of indication or ecological optimum values (ter Braak & Looman 1986). Based on the criteria given above, each species was classified as either a subordinate species (SO), a local dominant (LD) or a global dominant (GD). Differences between these three groups in successional and elevational position of the component species were tested by one-way analysis of variance, followed by Tukey contrasts.

Results

The fit of the regression was very good for almost all species, showing that dominance and presence are clearly related, and that the form of the relationships was quite different among species (Fig. 2). The early successional species *Puccinellia*, *Suaeda* and *Spergularia* were clearly local dominants which only achieved dominance when present in most of the plots in a habitat. The late succes-

Table 1. Regression parameters and R^2 for the dependence of the proportion of plots in which a species is dominant on the proportion of plots in which a species is present, across 15 habitats on a salt marsh (see Eq. 1 and Fig. 1). Also indicated is the elevational and successional position of each species, calculated as the weighted average of elevation and years in which the species has been found ($n=3927$).

Species	M/D ¹	A/P ²	Max. plant height ³ (m)	Successional position (yr)	Elevational position (m + MHT ⁴)	Regression parameters ⁵			Dominance type
						L	G	R^2	
<i>Salicornia europaea</i>	D	A	0.40	29	0.37	0.093	9.017	0.98***	SO
<i>Puccinellia maritima</i>	M	P	0.70	32	0.40	0.561	1.534	0.96***	LD
<i>Suaeda maritima</i>	D	A	0.50	32	0.48	0.777	4.384	0.88***	LD
<i>Juncus gerardi</i>	M	P	0.50	50	0.53	0.287	2.478	0.54**	SO
<i>Glaux maritima</i>	D	P	0.30	36	0.55	0.279	0.754	0.58***	SO
<i>Spergularia maritima</i>	D	P	1.00	30	0.56	0.715	4.168	0.98***	LD
<i>Limonium vulgare</i>	D	P	0.50	38	0.57	0.739	3.373	0.73***	LD
<i>Atriplex portulacoides</i>	D	P	1.50	38	0.65	0.477	8.456	0.67***	SO
<i>Plantago maritima</i>	D	P	0.60	33	0.73	0.648	2.729	0.86***	LD
<i>Artemisia maritima</i>	D	P	0.60	46	0.74	0.728	1.404	0.73***	GD
<i>Festuca rubra</i>	M	P	0.90	42	0.76	0.856	0.908	0.74***	GD
<i>Armeria maritima</i>	D	P	0.50	33	0.83	0.927	7.824	0.92***	LD
<i>Elymus athericus</i>	M	P	1.20	48	0.86	0.892	1.796	0.92***	GD

¹M = Monocot; D = Dicot; ²A = Annual; P = Perennial; ³According to van der Meijden (1990); ⁴Mean high tide; ⁵ = See eq. 1; ** $P < 0.01$; *** $P < 0.001$.

Fig. 2. Proportional dominance of 13 salt marsh species as dependent on the proportional presence across a range of habitats. See Table 1 for parameters and R^2 values of the regressions.

sional perennials *Artemisia*, *Festuca* and *Elymus* were clear examples of global dominants, which became dominant in the same proportion of plots of a habitat as in which they were present. Clear subordinates in this range of habitats were *Salicornia* and *Glaux*.

All species were classified into one of these three dominance types based on the criteria given in the methods, and the result is given in Table 1. The three dominance types differed significantly in their successional position ($F_{2,10} = 5.48$, $P = 0.025$). The global dominant species occurred later in the succession than the local dominants, while the subordinate species were in between and not significantly different from these two groups (Fig. 3).

The elevational position was almost significant between the three groups ($F_{2,10} = 3.52$, $P = 0.07$). The Tukey test revealed significant differences where global dominants occurred higher on the elevational gradient than subordinate species. Local dominants had an intermediate position.

Discussion

The relationships between the proportional presence and proportional abundance of salt marsh species across habitats were remarkably good, and showed different

types of relationships between species. The method therefore seems to work well to explore certain features of the dominance types present in a set of plant species. The differences between the dominance types in elevational and successional position of the species may help to understand which traits characterise the species of each group, and which processes are structuring these communities. Global dominants occurred later in the succession. This may be due to a trade-off between colonisation ability and competitive ability (Tilman 1993). Species which are good competitors because they invest in stems, height growth and vegetative storage (as *Artemisia* and *Elymus*) may have difficulty in invading a community very rapidly, because they produce less seeds, have poor dispersal, or have difficulty in establishing from seeds once arrived. A high potential dispersal as derived from data on floating and standing seeds and deposited driftline material (Bakker et al. 1985; Huiskes et al. 1995) is expected in the annual pioneer species *Salicornia*, *Spergularia*, *Limonium*, *Festuca* and *Elymus*. These authors found a low potential dispersal in *Puccinellia*, *Plantago*, *Artemisia* and *Armeria*. This may imply that the late successional position of *Elymus* is not due to dispersal limitation, but to some other factor, e.g. competition during the establishment phase.

Interestingly, local dominants (such as *Suaeda* and *Plantago*) were on average the first to appear in the

Fig. 3. Differences between three groups of dominance types of plant species in elevational and successional position on a salt marsh. Means with the same letter are not significantly different (Tukey test after one-way analysis of variance).

succession. These species which probably can invade very quickly and reach high abundances, but can not hold on to their dominant position very long. Species which occurred lowest on the salt marsh (the most salt tolerant species, as *Puccinellia* and *Salicornia* (Rozema et al. 1985) were generally the subordinate species in these communities, while global dominants occurred highest on the marsh. This is in accordance with the idea that species that adapt to very harsh conditions are generally poorer competitors. A general dogma of salt marsh zonation is that the lower vertical limit of species is controlled largely by tolerance of tidal factors, while the upper limit is fixed by interspecific competition (Snow & Vince 1984; Gray 1992; Pennings & Callaway 1992). This view is thus confirmed from the observed presence-dominance relationships of the species.

It should be noted that any definition of dominant and subordinate species is scale-dependent. We chose to analyse dominance at a 1-m² plot size, since we think that this is the scale at which interspecific competition occurs. Analyses of co-occurrences of species over larger spatial scales are expected to yield different results.

Most studies analysing large data sets of species occurrences aim at finding so-called assembly rules for communities (Connor & Simberloff 1979; Wilson 1989; Drake 1990; Smith et al. 1995). Assembly rules are thought to structure communities, meaning that the species are a non-random subset of the regional pool of species (Pimm 1991, p.189; Law & Morton 1996). Therefore, permutation tests are often used to detect significant deviations from random occurrences of species. The bottom line of the approach has been that species that are more alike in resource use (guilds, c.f. de Kroon & Olff 1995) are expected to co-occur less on

small spatial scales since they will outcompete each other. Therefore, this approach has been used to infer conclusions about the importance of competition in structuring community composition (Wilson & Gitay 1995; Stone & Roberts 1992). However, the appropriate null models are still debated (Wilson & Roxburgh 1995; Fox & Brown 1995).

An other approach to identify the forces at work in structuring plant communities has been followed by Keddy and co-workers (Keddy 1992; Wisheu & Keddy 1992; Keddy & Shipley 1989; Keddy et al. 1994) who studied experimentally derived competition matrices. These authors conclude that plant species are often arranged in a fixed order of competitive ability from good to bad, rather irrespective of the habitat characteristics. They explain the differential dominance of plant species in different habitats by differences in tolerance to adverse environmental conditions. A habitat type without any unfavourable conditions to plants is termed a core habitat, in which one or a few core species dominate. These core species are especially good competitors for light. Species occupying the unfavourable habitats (wet, acid, saline, etc.) are termed satellite species. A problem with the experimental derivation of competition matrices is that it is subject to practical constraints regarding the length of the study and the number of species that can be investigated. Pairwise competition studies involving a large number of species are never maintained longer than a few months (see, e.g. Keddy et al. (1994)). Good competitors in these experiments will be species that do well during the early dynamics of the competitive interactions, when plants mainly struggle for light. In the long run, poor light competitors can, however, outcompete these good light competitors, but this may take several years (Tilman & Wedin 1991). Nevertheless, the global dominants as identified in our study are expected to correspond to the species at the top of the competitive rankings as observed by Keddy et al. (1989, 1994). Species at the bottom of their rankings may be either local dominants in a different (adverse) habitat or intrinsically subordinate species.

We suggest that the method proposed in this paper may provide some insight into the relative importance of competition and dispersal in determining the abundance of plant species across a range of habitats. This may help in designing management practices aimed at restoration of species-rich plant communities, e.g. through lowering the intensity of competition for light (grazing, mowing) or through enhancing seed dispersal across habitats (re-introducing grazers or flooding) (Olff & Ritchie 1998).

We advocate that a joint analysis of species co-occurrences, competition experiments and presence-dominance relationships is a powerful tool for unravelling the processes at work that structure plant communities.

Acknowledgements. We thank Jelte van Andel, Tomáš Herben and Eddy van der Maarel for valuable comments on an earlier draft of this manuscript.

References

- Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. *Annu. Rev. Ecol. Syst.* 16: 39-61.
- Austin, M.P. 1986. The theoretical basis of vegetation science. *Trends Ecol. Evol.* 1: 161-164.
- Bakker, J.P., Russchen, P.T. & Dijkstra, M. 1985. Dispersal, germination and early establishment of halophytes and glycophytes on a grazed and abandoned salt marsh. *New Phytol.* 101: 291-308.
- Connor, R.K. & Simberloff, D. 1979. The assembly of species communities: chance or competition? *Ecology* 60: 1132-1140.
- de Kroon, H. & Olff, H. 1995. On the use of the guild concept in plant ecology. *Folia Geobot. Phytotax.* 30: 519-528.
- Drake, J.A. 1990. Communities as assembled structures: do rules govern pattern? *Trends Ecol. Evol.* 5: 159-164.
- Fox, B.J. 1987. Species assembly and the evolution of community structure. *Evol. Ecol.* 1: 201-213.
- Fox, J.B. & Brown, J.H. 1995. Reaffirming the validity of the assembly rule for functional groups or guilds: a reply to Wilson. *Oikos* 73: 125-132.
- Goldberg, D.E. 1995. Generating and testing theory about community structure: which theory is relevant and can it be tested with observational data? *Folia Geobot. Phytotax.* 30: 511-518.
- Gray, A.R. 1992. Salt marsh plant ecology: Zonation and succession revisited. In: Allen, J.R.L. & Pye, K. (eds.) *Salt marshes: morphodynamics, conservation and engineering*, pp. 63-79. Cambridge University Press, Cambridge.
- Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242: 344-347.
- Grime, J.P. 1984. Dominant and subordinate components of plant communities: implications for succession, stability and diversity. In: Gray, A.J., Crawley, M.J. & Edwards, P.J. (eds.) *Colonizations, succession and stability*, pp. 413-428. Blackwell Scientific Publications, Oxford.
- Grime, J.P., Crick, J.C. & Rincon, J.E. 1986. The ecological significance of plasticity. *J. Exp. Biol.* 7: 5-29.
- Hodgson, J.G. 1986. Commonness and rarity in plants with special reference to the Sheffield flora Part I: The identity, distribution and habitat characteristics of the common and rare species. *Biol. Conserv.* 36: 199-252.
- Huiskes, A.H.L., Koutstaal, B.P., Herman, P.M.J., Beetink, W.G., Markusse, M.M. & De Munck, W. 1995. Seed dispersal of halophytes in tidal salt marshes. *J. Ecol.* 83: 291-308.
- Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3: 157-164.
- Keddy, P.A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. *Oikos* 54: 234-241.
- Keddy, P.A., Twolanstrutt, L. & Wisheu, I.C. 1994. Competitive effect and response rankings in 20 wetland plants: Are they consistent across three environments? *J. Ecol.* 82: 635-643.
- Law, R. & Morton, R.D. 1996. Permanence and the assembly of ecological communities. *Ecology* 77: 762-775.
- Olff, H., Bakker, J.P., Platerink, R.J., van Wijnen, H. & De Munck, W. 1997. Vegetation succession and herbivory on a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814.
- Olff, H. & Ritchie, M.E. In press. Effects of herbivores on grassland plant diversity. *Trends Ecol. Evol.* 13.
- Pennings, S.C. & Callaway, R.M. 1992. Salt marsh plant zonation - the relative importance of competition and physical factors. *Ecology* 73: 681-690.
- Pimm, S.L. 1991. *The balance of nature? Ecological issues in the conservation of species and communities*. University of Chicago Press, Chicago, IL.
- Platt, W.J. & Weiss, I.M. 1985. An experimental study of competition among fugitive prairie plants. *Ecology* 66: 708-720.
- Rabinowitz, D. 1981. Seven forms of rarity. In: Synge, H. (ed.) *The biological aspects of rare plant conservation*, pp. 205-218. John Wiley, Bath, Avon.
- Rastetter, E.B. & Shaver, G.R. 1996. Functional redundancy and process aggregation: linking ecosystems to species. In: Lawton, J.H. (ed.) *Linking species and ecosystems*, pp. 215-223. Chapman and Hall, New York.
- Rozema, J., Bijwaard, P., Prast, G. & Broekman, R. 1985. Ecophysiological adaptations of coastal halophytes from foredunes and salt marshes. *Vegetatio* 62: 499-521.
- Smith, B., Mark, A.F. & Wilson, J.B. 1995. A functional analysis of New Zealand alpine vegetation: variation in canopy roughness and functional diversity in response to an experimental wind barrier. *Funct. Ecol.* 9: 904-912.
- Snow, A.A. & Vince, S.W. 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. *J. Ecol.* 72: 669-684.
- Stone, L. & Roberts, A. 1992. Competitive exclusion, or species aggregation. *Oecologia (Berl.)* 91: 419-424.
- ter Braak, C.J.F. & Looman, C.W.N. 1986. Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio* 65: 3-11.
- Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58: 3-15.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* 74: 2179-2191.
- Tilman, D. & Wedin, D. 1991. Dynamics of nitrogen competition between successional grasses. *Ecology* 72: 1038-1049.
- van der Meijden, R. 1990. *Heukels' Flora van Nederland*. 21st ed. Wolters-Noordhoff, Groningen.
- Wilson, J.B. 1989. A null model of guild proportionality, applied to stratification of a New Zealand temperate rain forest. *Oecologia (Berl.)* 80: 263-267.
- Wilson, J.B. & Gitay, H. 1995. Limitations to species coexistence: evidence for competition from field observations, using a patch model. *J. Veg. Sci.* 6: 369-376.
- Wilson, J.B. & Roxburgh, S.H. 1995. A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. *Oikos* 69: 267-276.
- Wisheu, I.C. & Keddy, P.A. 1992. Competition and centrifugal organization of plant communities: theory and tests. *J. Veg. Sci.* 3: 147-156.

Received 10 February 1998;

Revision received 20 April 1998;

Accepted 6 May 1998.