

1 Original Research Article

2 **Effects of forest succession on the occurrence of two orchid** 3 **species on Terschelling the Netherlands**

4 **ABSTRACT**

5 On the island of Terschelling (NL) two rare orchids' species (*Neottia cordata* and *Goodyera repens*)
6 occur in the homogenous *Pinus nigra* stands. The forest is owned by the State Forestry Service which
7 aims to preserve the orchids by maintaining the current forest as it is without any management. This is
8 contradictive to the general management goals of more mixed forests with high biodiversity. Therefore
9 our research question is: "What environmental factors are determining the occurrence of the orchid
10 species *G. repens* and *N. cordata* in the forests on Terschelling and how these factors can be
11 preserved in a mixed forest with a diverse forest structure?" The fieldwork took place in the
12 Hoornsebos Vegetation composition, forest structure and composition, humus and litter layer, and
13 light environment were measured. Occurring plant communities consisted of Vaccinio-Piceetalia and
14 Quercetalia-roboris. Both *N. cordata* and *G. repens* occurred in frequent numbers in the Vaccinio-
15 Piceetalia community, but were rare in the Quercetalia-roboris. Our results show that both orchids'
16 species are dependent on the occurrence of needle litter and need to grow in low productive
17 environment where they are not outcompeted by other plants. In the forest there is a general trend of
18 development towards more broadleaved tree composition which has a negative effect on the
19 occurrence of both orchid species. The development of a shrub layer leads to increased shading and
20 canopy closure and will decrease *N. cordata* abundance. Aging of coniferous forests will lead to
21 further build-up of the litter layer which negatively affects *G. repens*. Without management the suitable
22 conditions will slowly disappear for both *G. repens* and *N. cordata*, so active management is required
23 for sustainable conservation of the orchid species.

24 *Keywords: Terschelling, Pinus nigra, Neottia cordata, Goodyera repens, mixed forest, broadleaved*
25 *forest, forest succession, orchid abundance.*

26 **1. INTRODUCTION**

27 In the planted  *Pinus nigra* forests of the Dutch Wadden island of Terschelling the orchid species
28 *Neottia cordata* and *Goodyera repens* occur. Both of these orchid species occur in large parts of
29 Europe ([26]; [34]) and North America [11], but are rare in the Netherlands [12]. *G. repens* also occurs

on the mainland of the Netherlands along the Dutch west coast and locally in more inland pine forests [12]. *N. cordata* is apart from the Wadden islands, only found on two locations on the mainland [12]. The indication of both species on the Dutch red list for vascular plants is sensitive [20]. The species are on the Dutch target species list for nature management because of their rarity in the Netherlands [2]. Both *G. repens* as *N. cordata* are bound to coniferous forests. The occurrence of micro-habitat with a relatively moist needle litter layer s is crucial for the orchids [38].

The State Forestry Service (NL: Staatsbosbeheer; SBB) wants to maintain the orchid species in the forests on Terschelling. To keep the forests suitable for *G. repens* and *N. cordata* SBB designated core areas where they do not apply any management to preserve the pure *Pinus nigra* forests [41]. The cover of both *G. repens* and *N. cordata* is high in these forests, but apart from these species the forest is relatively species poor [18]. Also the recreational value of these forests is low because of the lack of variation in structure and light environment [3]. In general high species diversity and recreational and aesthetic value of forests are important goals for SBB [33]. Apart from the SBB goals the island of Terschelling is ranked as a Natura 2000 area. The *G. repens* and *N. cordata* are although no specific target species within the Natura 2000 management plan, but there is a maintenance obligation for the habitat (H2180_A, Dry forests of the dunes) in where the species occur [21].

For high species diversity as desired by SBB and Natura 2000, forests should consist of mixed forests with broadleaved trees [5] and parts of the forest structure should be more open and include gaps ([35]; [31]). Also for the recreational value of forest mixed and a more variable forest structure is important [4]. However the requirements on structure and species composition for this habitat type are not suitable for *G. repens* and *N. cordata* because of the requirements on high occurrence of broadleaved trees and a more open forest structure [21]. This is in conflict with the requirements of *G. repens* and *N. cordata*. Therefore the SBB management on *G. repens* and *N. cordata* to maintain the status in the unmixed, even-aged *Pinus nigra* forests are conflicting with the other goals of SBB and the goals of Natura 2000 in the forests on Terschelling. Also the management will not be effective on the long term since already in the unmanaged forests broadleaved species establish in the understory [18].

Hence, this research aims to gain insight in the environmental factors that determine the occurrence of the orchid species *G. repens* and *N. cordata* in forests on Terschelling. The research will result in a

60 better understanding of how these factors change when forest composition changes due to
 61 succession and forest dynamics. When there is an understanding of these factors, the possibilities of
 62 maintaining the orchid species (both in space as in time) in a mixed forest with a diverse structure can
 63 be explored. The goal of our research is to come to management recommendations that influence the
 64 forest structure and composition with respect to the natural forest dynamics and succession in a way
 65 that the environmental circumstances are suitable for the orchids and other goals of the forest
 66 management can also be met. To come to appropriate recommendations considering the
 67 management of the forests the following research question is addressed in this paper

68 “What environmental factors are determining the occurrence of the orchid species *G. repens* and *N.*
 69 *cordata* in the forests on Terschelling and how can these factors be preserved in a mixed forest with a
 70 diverse forest structure?”

71 The research question consists of three parts: the vegetation (abundance of *G. repens* and *N.*
 72 *cordata*), the environmental factors determining the vegetation and the forest structure and
 73 composition. This is visualized in figure 1; the relationships in this figure are simplified to make the
 74 theoretical framework applicable in our research. In this theoretical framework  the vegetation and the
 75 abundance of orchids is a result of environmental factors. Dispersal is not taken into accounts
 76 because in general this is not considered as a problem for orchids ([1]; [28]). However the occurrence
 77 of orchid species indeed will be affected by the interaction of biotic factors (forest structure and
 78 composition) and abiotic factors (climate, soil, soil moisture and pH) (Figure 1.). More importantly, the
 79 forest structure is influencing the environmental factors by shading, recruitment and production of litter
 80 in certain quantities and of certain quality. The forest structure and composition is constantly changing
 81 due to succession, degradation, forest dynamics and recruitment of trees. These processes are again
 82 influenced by the environmental factors in the forest. The forest development can be accelerated,
 83 adjusted or slowed down by forest management

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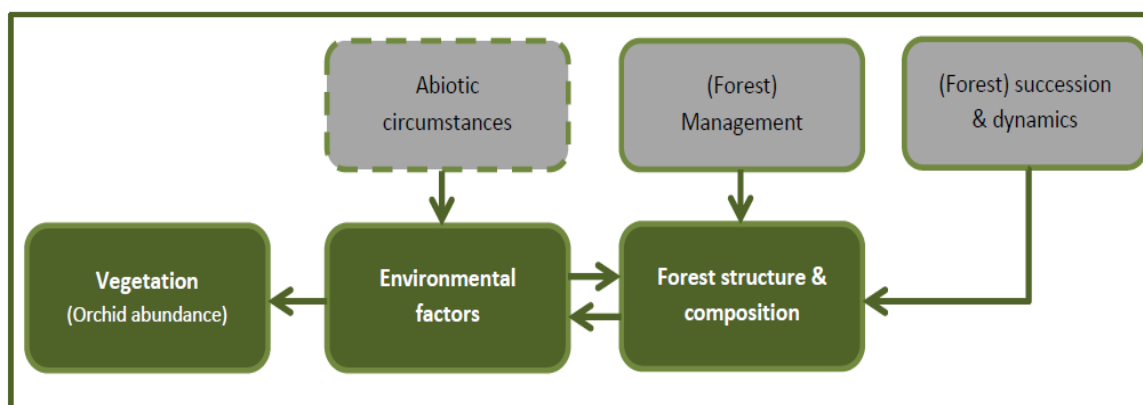


Fig.1. Theoretical framework (Simplified) relation between forest structure and composition, environmental factors and the vegetation and the effect of abiotic circumstances, forest management and forest succession and dynamics

2. MATERIALS AND METHODS

To answer the formulated research question, three forest types were identified and located in the “Hoornse bos” on Terschelling (Centre of the “Hoornse bos”: 53.406181 N, 5.344591 E). The site was selected based on the following criteria: pure coniferous forest (Basal area *Pinus nigra* > 85%), broadleaved forest (Broadleaved species (mostly *Quercus robur* and some *Fagus sylvatica*) > 70%) and mixed coniferous and broadleaved forest (Mostly *Pinus nigra* and *Quercus robur*). Out of these selected three forest types, 11 relevés were systematically selected which further divided to 10 x 10 m and 4 x 4 m relevé size. At all sites, elevation (valley, slope or hill) was noted to exclude it as a confounding factor. We measured in the relevés vegetation composition (including orchid abundance), forest structure and composition, humus and litter layer and light environment. Also we took soil samples to the Wageningen UR laboratory to test for soil organic matter, soil moisture content and electric conductivity.

Vegetation composition

In the center of the plot, a 4 x 4 m relevé was situated where the presence and abundance of vascular plants and mosses were recorded using the ordinal scale of Braun-Blanquet [6]. The abundance of *G. repens* and *N. cordata* was recorded using a classification (0 = 0, 1 = 1-10, 2 = 11-50, 3 = 51-100, 4 = 101-300, 5 = >300). Apart from the presence and abundance per species the total cover of vegetation, moss, litter and bare soil was recorded. The vegetation data was used to classify

the relevées into vegetation communities. The orchids were counted to relate the environmental factors in a relevée to the abundance of orchids

Forest structure and composition

The forest structure in the plots was measured to relate the environmental factors to the forest structure and composition. Also the forests composition in a plot was used to classify a plot as coniferous, mixed or broadleaved forest. The forest structure and composition was measured by measuring the basal area ($\text{m}^2/\text{ha}/\text{species}$), seedlings and shrubs in 10 x 10 m plot and canopy openness (%).

Basal area was measured by the Bitterlich method using a relascope [4]. The Bitterlich method is a commonly used method in forestry to measure forest density and composition. Also it helps to gain insight into the openness of a stand although it does not take the shrub layer into account (which actually is very relevant for the orchids). The method is not very precise, especially when stands become more mixed and uneven aged, but the uncertainty in the method is acceptable in the homogeneous pine forests because they are very even aged. The basal area was used to classify the plots as coniferous, mixed or broadleaved and to relate the occurrence of vegetation to the forest composition.

A 10 x 10 m plot was placed in every plot to measure the forest composition. The presence and abundance of trees, shrubs and tree seedlings (> 0.5 m) was recorded using the ordinal scale of Braun-Blanquet (1951). It was also recorded whether trees were present in the canopy. The data was used, together with the data from the 4 x 4 relevées, to classify the relevées into plant communities. Also the data was used to gain insight into the spontaneous development of the forest and to relate environmental factors and orchid presence with forest composition in a plot.

The canopy openness was assessed using photos of the canopy of every plot (see figure 2). Pictures were taken at 30 cm height with a Canon D70 using a Sigma 4.5 mm circular fish-eye lens. Canopy openness was used to relate forest structure to forest composition and light availability for the vegetation under the canopy.

Humus and litter layer

In all plots the thickness of the humus and litter layer was measured. Also the composition of the litter with respect to presence of needles was assessed. Samples of the humus were taken to measure moisture content (%), pH, electronic conductivity ($\mu\text{S}/\text{cm}$) and organic matter content (%).

137 The focus on the litter and humus layer instead of the soil as a whole is because both *G. repens* and
138 *N. cordata* root exclusively in the litter and humus layer [38].

139 Samples were taken at the same day in a short moment of time. Moisture content was measured by
140 comparing the fresh weight of the samples with the dry weight. The humus pH was measured by
141 mixing (shaken for an hour) 20 gr of the sample with 50 gr of distilled water and measuring the pH
142 and electronic conductivity of the mixture. Organic matter content was measured using the loss on
143 ignition method [15].

144 The data was used to relate the forest structure and composition to the litter and humus traits. Also
145 the effect of the litter and humus traits on the vegetation and the abundance of *G. repens* and *N.*
146 *cordata* was assessed.

147 **Light environment**

148 The Photosynthetic Active Radiation (PAR) under the canopy was measured using a SunScan
149 Canopy Analysis System [37]. The SunScan, with the one meter long probe, was used two times for
150 every plot. Pointing is done alternatively one time pointing to north and one time east. The time of
151 measurement was noted for every plot. Control values were measured in the open dunes every five
152 minutes to correct for light intensity changes over day. The unit we used was remaining light under the
153 canopy (in comparison to the control).

154 The light measurements were used to relate light environment to the forest structure and composition
155 and the vegetation and abundance of *G. repens* and *N. cordata*.

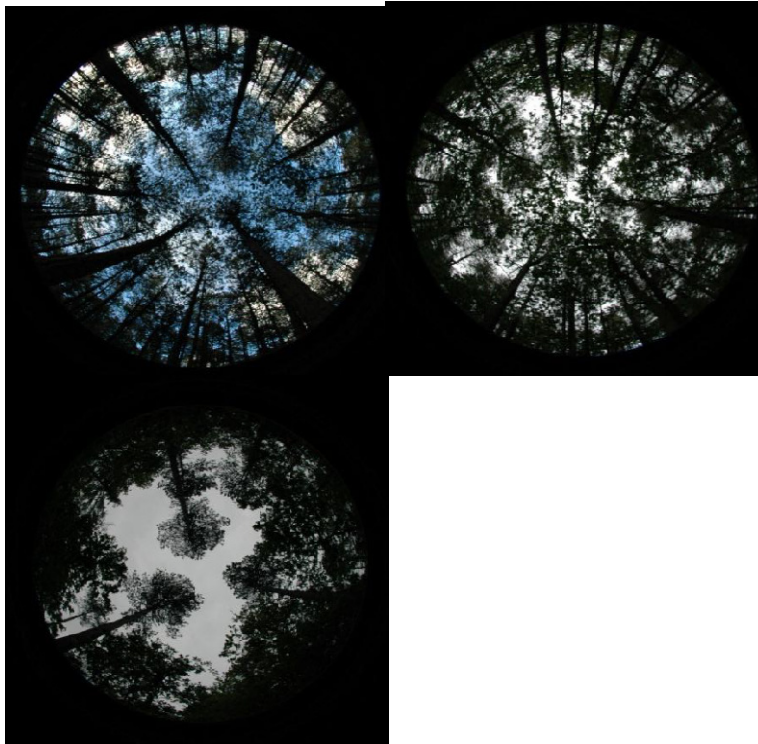


Fig.2. Canopy pictures of (1) coniferous forest, (2) broadleaved forest and (3) an open mixed forest

2.1 Data analysis

The collected data was analyzed using Microsoft Excel, IBM SPSS Statistics 19, TWINSpan (Hill 1979) and TurboVeg [16]. The procedure is discussed per parameter.

Vegetation composition

The vegetation data was classified using TWINSpan [17] and determined with the help of 'Veldgids Plantengemeenschappen' [30]. The distribution of the plant communities and the orchid abundance classes over the forest types was tested using a Pearson Chi-square test. The Ellenberg indicator values [9] per plant community were calculated using TurboVeg [16].

Forest structure and composition

The result from basal area measurements, the 100 m² plot and the canopy openness were analyzed and statistically tested using IBM SPSS Statistics 19 and Microsoft Excel. Since most of the data was multivariable and consisted of more than two groups we used Two-Way-ANOVA. The abundance data was tested using a Pearson Chi-square test. The Canopy photos were analyzed using Gap Light Analyzer software [13] to calculate the canopy openness.

To test for the effect of the canopy openness on the vegetation  we transformed the abundance data of the two orchids into absence/presence data and performed a logistic regression on the data.

Humus and litter layer

To statistically test the litter traits  we used a Two-Way ANOVA with the forest types and the plant communities as groups and the different traits as independent variables. To test for the effect of the different litter traits on the presence of the orchids we used the presence/absence data of the orchids to perform logistic regression with the litter traits as independent variables *Light environment*

To test for the relation between remaining light under the canopy and with canopy openness and basal area we used regression. For testing the differences between different forest types and plant communities we used Two-Way ANOVA with the remaining light as independent variable.

3. RESULTS

The results are discussed per parameter and presented with the questions in 

Vegetation composition

Based on the vegetation releveés  we can distinguish two plant communities. In 14 releveés  we found the Vaccinio-Piceetalia (41A) which is a typical plant community for coniferous forests. Both *G. repens* and *N. cordata* occur in 13 out of 14 of the releveés classified as Vaccinio-Piceetalia community. *G. repens* is limited to this plant community and does not occur in the other releveés. *Pinus nigra* is in general the dominant tree species in the canopy above the releveés containing the Vaccinio-Piceetalia, but some releveés also have broadleaved *Quercus robur* or *Fagus sylvatica* in the canopy. A further distinction of the Vaccinio-Piceetalia is not possible because we have not found enough differential species. This is a common problem in Vaccinio-Piceetalia vegetation because most of the typical coniferous bound plant species are too rare for classifying vegetation [36]. The vegetation in the other 17 releveés was classified as Quercetalia-roboris (42Aa) which is a typical plant community for broadleaved forests [36]. Also here further classification was not possible because of the low amount of differencing species. *N. cordata* does occur in this vegetation type, but does not make the same abundances as it does in the Vaccinio-Piceetalia.

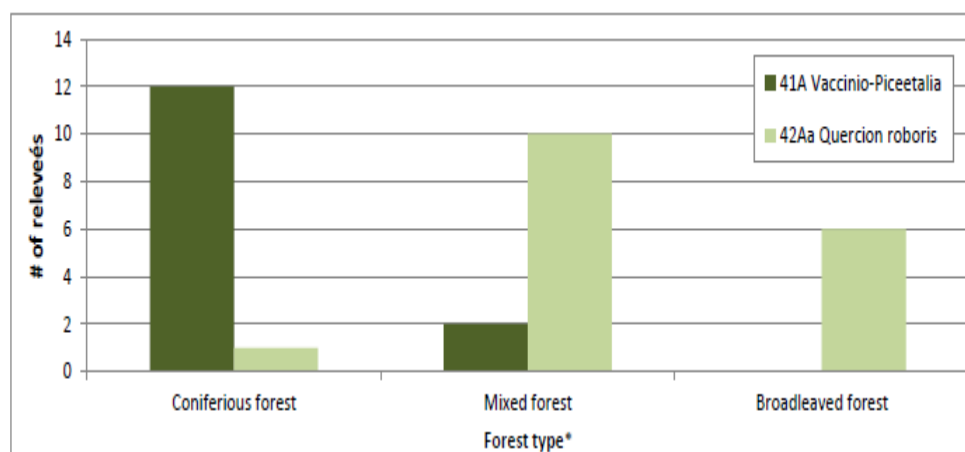


Fig. 3. Distribution of plant communities over forest types ($\chi^2=28.4$, $df=2$, $p=.01$).

***Forest types based on basal area per species (Coniferous *Pinus nigra* > 85%; Broadleaved Br. Leaved species > 70%; Mixed forest is remaining relevés)**

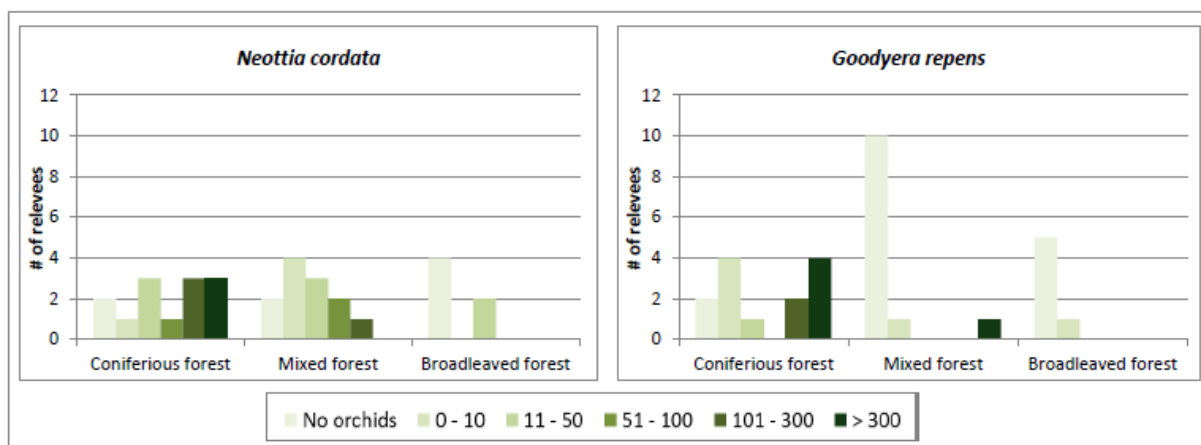
The Ellenberg indicator values [9] between the two plant communities are more or less similar. Both plant communities are bound to the forest and grow in more or less the same abiotic circumstances. This explains the similarity in Ellenberg values.

When we look to the distribution of the plant communities over the forest types in Figure 3 we see that the Vaccinio-Piceetalia community, where both *G. repens* and *N. cordata* occur, occurs in both coniferous forest as in mixed forest but does not occur in broadleaved forest. Vaccinio-Piceetalia does mostly occur in coniferous forest ($\chi^2=28.4$, $df=2$, $p<0.01$). The two relevés of Vaccinio-Piceetalia in the mixed forest both contain *G. repens* as well as *N. cordata*. Figure 3 also suggests that as soon a forest becomes more mixed a Quercetalia-roboris vegetation develops and *G. repens* and *N. cordata* disappear. Figure 4 shows the abundance of *G. repens* and *N. cordata* distributed over the forest types. We can see that *N. cordata* occurs both in coniferous forests as in mixed forests, but reaches the highest abundances in coniferous forests ($\chi^2=21.23$, $df=10$, $p=.03$). *G. repens* does not reach the same abundances as *N. cordata* does and is even more bound to the coniferous forest ($\chi^2=64.9$, $df=10$, $p=.01$).

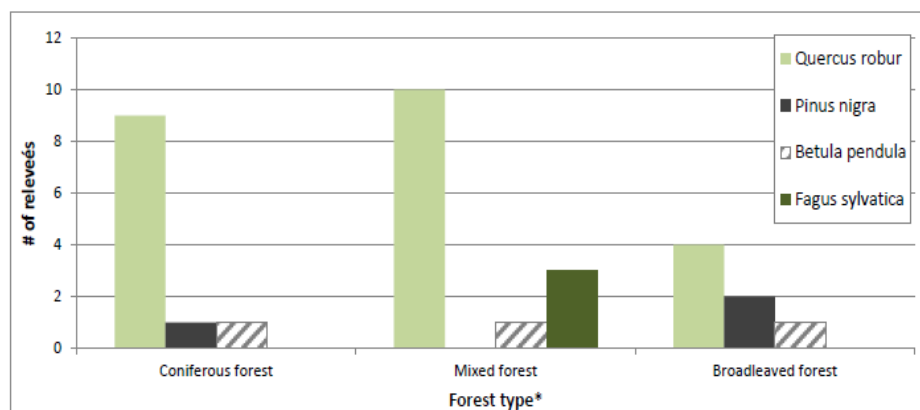
Forest structure and composition

The average basal area in the relevés is 26.8 m²/ha ($\pm$ 7.8 m²/ha), this is low in comparison with Dutch yield tables where the basal area in comparable forests is set around 32 m²/ha [19]. These

220 tables are although based on even-aged monocultures where basal area is higher because of the
221 higher tree density. There is no significant difference in basal are per forest type or plant community.



222
223 **Fig. 4. Distribution of abundance classes over forest type for *N. cordata* ($\chi^2=21.23$, $df= 10$,**
224 ***p*=.03) & *G. repens* ($\chi^2=64.9$, $df=10$, *p*=.03).**



225
226 **Fig.5. Occurrence of tree seedlings over the 16 m² relevés over forest types ($\chi^2=41.6$, $df=6$,**
227 ***p*=.01).**

228 ***Forest types based on basal area per species (Coniferous *Pinus nigra* > 85%; Broadleaved *Br.***
229 ***Leaved species* > 70%; Mixed forest is remaining relevés)**

230 In general the trees that are found in the canopy in the 100 m² relevé have been planted, except for
231 some of the mixed forests where broadleaves have spontaneously reached the canopy (i.e.
232 sometimes also by liberation through thinning). Seedlings under the canopy have although
233 spontaneously colonized the area and are a good indicator for the suitability for different tree species.
234 In the 16 m² relevés we have recorded all seedlings under 0.5 m present in the relevé. Figure 5

shows the results of the tree seedlings in these plots. We can see that *Q. robur* is colonizing most of the plots irrespective whether *Q. robur* is present in the canopy or not ($\chi^2=41.6$, $df=6$, $p=.01$). *P. nigra*, *B. pendula* and *F. sylvatica* are barely found in the relevés. The result of Figure 5 shows that, without management, the forest is developing in the direction of a broadleaved oak forest.

The canopy openness of the plots was on average 21% (± 7). The comparison between forest types suggests that coniferous forests are more open and broadleaved forests have the most closed canopy. After testing this was not significant ($F_{2, 28} = 3.314$, $P=.051$) but the difference between coniferous and broadleaved, without mixed forest was. The measurement of canopy openness was taken at 30 cm height and therefore takes the shrub layer into account, the shrub layer seems to explain the more closed canopy in broadleaved forests partly (see also results of light environment). When we look at the occurrence of *G. repens* and *N. cordata* as a result of the canopy openness we do not find any significant effect of canopy openness on *G. repens*. *N. cordata* is although more probable to grow when the canopy is more open (Wald= 6.975, $df = 1$, $p = .03$). Figure 6 shows this effect.

Humus and litter layer

On average the humus thickness is 6.7 cm (± 1.9 cm). The thickness is significantly lower in coniferous forests in comparison to broadleaved and mixed forests ($F_{2, 28} = 7.88$, $P < 0.05$), but there is no difference in the litter layer (average litter thickness 1.7 cm ± 1.1 cm). In the coniferous forests we observed a sharp gradient between the litter layer, the thin humus layer and the mineral soil. In the broadleaved forests we found this gradient was much more gradual. This suggests that the decomposition of litter is higher in the broadleaved forest than it is in the coniferous forest. Although we did not find a significant difference in organic matter concentration of the humus, we assume that there is more organic matter available for plants in the broadleaved forest because the thickness of the humus layer is bigger. That we did not find a significant difference in litter layer is probably due to the lower litter production in coniferous forest compared to broadleaf forest, because coniferous trees have a longer leaf life span and therefore a lower litter production [29].

Despite the higher decomposition rates in the broadleaved forest the pH of the humus was slightly lower in the broadleaved forest ($F_{2, 28} = 15.634$, $p=.01$), this might be due to leaching of cations in the humus layer of Broadleaved forests.

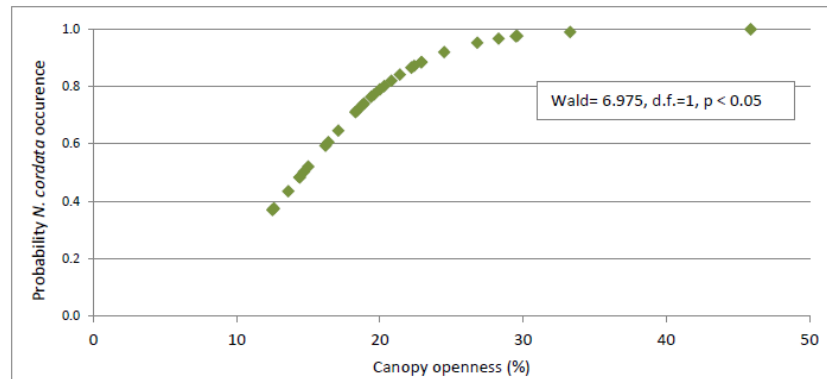


Fig.6. Probability of occurrence of *N. cordata* as a result of canopy openness (Wald= 6.975, d.f.=1, p = .02).

The moisture content of the humus in broadleaved forest was although also higher ($F_{2,28}=4.362, p=.02$) which can have a positive influence on decomposition rates.

When we compare the litter from the two plant communities we see the same patterns. The *Quercetalia-roboris* plant community, which is more or less correlated with the occurrence of broadleaved forest, has higher moisture content ($F_{1,29}=4.565, p=.03$), lower pH ($F_{1,29}=37.378, p=.01$) and a thicker humus layer ($F_{1,28}=8.8416, P=.03$).

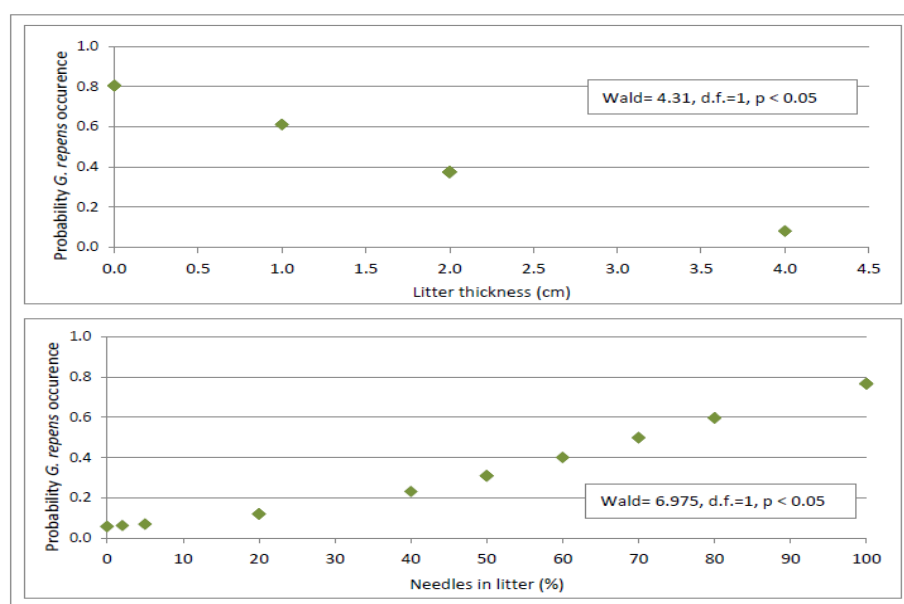
When we test for the effect of the different litter traits on the presence or absence of *G. repens* and *N. cordata* we do not find any significant effect on the presence of *N. cordata*. *G. repens* although is affected by the litter, the results of this are visualized in Figure 7a and 7b. When the thickness of the litter increases, the probability of *G. repens* occurring decreases (Wald= 6.975, df=1, p=.02). Also with an increase of the percentage of needles in the litter we have found an increase in the probability of *G. repens* occurring (Wald= 6.975, df=1, p=.03). We did not find any significant differences between forest types, orchid presence nor plant communities with respect to electronic conductivity.

Light environment

The remaining light under the canopy was very closely related to canopy openness ($R^2=0.79$; $y = 1.0012x - 0.1042$). The relation between remaining light and basal area is poor, partly because basal area does not take the shrub layer into account. The canopy of the broadleaved forest intercepts more light than mixed and coniferous forests. The most light can penetrate through the coniferous canopy ($F_{2, 28}=6.589, p=.03$).

4. DISCUSSION

287 *N. cordata* and especially *G. repens* are both differential species for the Vaccinio-Piceetalia plant
 288 community. This makes it hard to conclude that the orchids disappear as a result of the
 289 disappearance of the plant community because the community can simply no longer be identified
 290 because of the absence of *G. repens* and *N. cordata*. Apart from that the Ellenberg values of the
 291 Quercetalia-roboris, the replacing plant community, are that similar to the values of the Vaccinio-
 292 Piceetalia that is hard to draw conclusions based on the plant communities. Therefore it is better to
 293 take the environmental factors in the different forest types into consideration to explain the absence,
 294 presence and abundance of *G. repens* and *N. cordata* in the forest. Our results suggest that the
 295 mechanisms explaining the occurrence of the species differ partly for *G. repens* and *N. cordata*.



296

297 **Fig. 7. (a) Probability of occurrence of *G. repens* as a result of litter thickness (Wald= 4.31,**
 298 **d.f.=1, p=.02). (b) Probability of occurrence of *G. repens* as a result of % needles in litter**
 299 **(Wald= 6.975, d.f.=1, p= .02)**

300 *N. cordata* is affected by canopy openness and is more present and reaches the highest abundances
 301 in coniferous forest. It is difficult to disentangle the effect of broadleaved forest from the light/canopy
 302 openness effect on the *N. cordata* occurrence and probably both are important. The light availability at
 303 a site seems to be partly explaining the occurrence of *N. cordata*. Our results show that *N. cordata* is
 304 more likely to occur when the canopy is more open. We suspect that there will be some optimum
 305 somewhere and that at a certain moment the canopy will be too open and more productive plant
 306 communities will take over and *N. cordata* will be outcompeted [36]. We did not have enough relevés

307 in very open forests to test this, but we haven't observed *N. cordata* in forest gaps during our
 308 fieldwork. We have found no effects of canopy openness on *G. repens*.

309 When we look to the abundance of *N. cordata* the species do occur in broadleaved forests, but the
 310 abundance is much lower than it is in the coniferous forest, partly because broadleaved forests are
 311 darker than coniferous forests. *G. repens* does not occur in broadleaved forest. The difference in light
 312 environment can be explained by the shape of Pine trees which are more vertically organized and
 313 therefore more light gets through the canopy [14]. Other factors than light that are changing in
 314 broadleaved forests that might explain the decline of *N. cordata* and absence of *G. repens* are lack of
 315 pine needles and increased moisture and organic matter availability in broadleaved forests. Also pH
 316 differs between coniferous and broadleaved forest, but the difference is although considered to be too
 317 small to have any significant effect on the orchids and both forest types have acidic humus layer.

318 The humus in the broadleaved forests has higher moisture content and there is more organic matter
 319 available for plants. The higher moisture and organic matter availability in broadleaved forests create
 320 more chances for different plant species ([10]; [40]) and will lead to the *N. cordata* being outcompeted.

321 Whether this also takes place for *G. repens* is hard to judge whether we are not sure if the species
 322 even germinate in the broadleaved forest. In the literature the occurrence of needles in the litter is
 323 also considered to be important for *N. cordata* and *G. repens* ([26]; [11]; [34]). Also out of our results
 324 the presence of *G. repens* and *N. cordata* is most explained by the forests type and needles in the
 325 litter. We haven't found any explanation in the literature for the importance of the litter for *N. cordata*
 326 and *G. repens*, but we do see that abundance of the species is highest in pine forests. We
 327 hypothesise that the physical traits of needles containing litter might be important for the orchid to
 328 successfully germinate, grow and/or reproduce. Also the presence of specific mycorrhiza might be
 329 important for both the orchids. Litter of broadleaves is more horizontally oriented in comparison to
 330 needle litter and forming a sort of physical barrier [27]. This might be problematic for the orchids to
 331 penetrate with their roots through the litter layer. Also this will have an effect on the moisture
 332 availability and light penetration to the humus layer, making the broadleaved forest more suitable for
 333 other plants and increasing the competition on these sites. As soon as, the needle litter becomes less
 334 mixed this problem will be less important. This might explain the abundance gradient from coniferous
 335 forest and mixed forest to broadleaf forest.

Apart from the physical traits of the litter the presence of mycorrhiza might explain the presence of the orchids. Some orchids need specific mycorrhiza for germination of their seeds. We have found that *G. repens* is dependent on these mycorrhiza ([8]; [7]), but some papers suggest that actually all orchids have an obligate relationship with mycorrhiza for germination ([32]; [36]). When the orchids that are important for *N. cordata* and *G. repens* are limited in their presence to needle litter this limitation will also count for the orchids. In general more different mycorrhiza will occur in coniferous forests [39] which make this hypothesis more plausible. We cannot prove this hypothesis based on our results and further research on the relation between the mycorrhiza and the orchids is needed. The current management of the State Forestry Service does not seem to be effective to preserve the circumstances suitable for the occurrence of the orchids. No management in the monocultures of *Pinus nigra* will lead to a gradual development to more broadleaved forest with *Quercus robur* and on the long term *Pinus nigra* will disappear out of the forest system. The results from the vegetation recordings showed that this will lead to a shift from the Vaccinio-Piceetalia plant community to the Quercetalia-roboris plant community and a disappearance of the orchids *G. repens* and *N. cordata*. Also without regeneration of broadleaf forest the environment will become unsuitable for *G. repens* since in forests of *P. nigra* there will be a build-up of the litter layer [22]. Our results show that the probability of *G. repens* to found decreases when the litter layer increases. So when these *P. nigra* forests age they will become less suitable for *G. repens*. We haven't found evidence that this will also count for *N. cordata*.

The successful colonization of *Q. robur* might be explained by the closed canopy and the thick humus layer in the forest. *Q. robur*, in contrary to *P. nigra* and *B. pendula*, has big seeds which have enough reserves to get through the litter layer and is dispersed in a forest easy by birds and rodents ([24]; [36]). Also *Q. robur* is more shade tolerant than *P. nigra* and *B. pendula* and can cope (longer) with the shaded circumstances under the forest canopy [23]. The lack of regeneration of *F. sylvatica* is probably due to seed limitation due to lack of reproductive trees. For successful regeneration of *P. nigra* forest gaps should exists where the forest climate is interrupted and no litter layer is present. In these pioneer situations *P. nigra* can germinate and maintain itself [36].

5. CONCLUSION AND RECOMMENDATIONS

Both orchid species are dependent on the occurrence of needle litter and need to grow in a low productive environment where they are not outcompeted by other plants. The presence of mycorrhiza

is likely to be important for the species. For *N. cordata* it is also important that there is enough light available. For *G. repens* the litter layer should not be too thick. In general the development to more broadleaved forest has a negative effect on the environmental factors that stimulate occurrence of *G. repens* and *N. cordata*. The development of a shrub layer leads to increased shading and canopy closure and will decrease *N. cordata* abundance. Aging of coniferous forests will also lead to a further build-up of litter what eventually will lead to the disappearance of *G. repens*. In line with this the two mechanisms that eventually will lead to the decrease of *G. repens* and *N. cordata* are succession from planted coniferous forest with *P. nigra* to a mixed broadleaf forest with *Q. robur*, *F. sylvatica* and *B. pendula* and the build-up of the litter layer in the present *P. nigra* stands. For preservation of the suitable conditions for *G. repens* and *N. cordata* there needs to be a focus on regeneration of (patches of) unmixed *P. nigra* forests, without management the suitable conditions will slowly disappear and active management is required for sustainable conservation of the orchid species. The recommendations are written aimed at forest management focused on a sustainable conservation of *G. repens* and *N. cordata*, attaining a mixed, species rich forest attractive for recreants. These recommendations will possibly lead to a decrease of the total amount of individuals of *G. repens* and *N. cordata* in the forest, but will lead to a sustainable conservation of the species.

- Spread in space and time patches of forest should be removed (min. 2 x dominant tree heights) to create regeneration gaps specifically for *Pinus nigra* recruitment.
- The soil in the regeneration gaps should be scarified to make it possible for *P. nigra* to germinate and settle.
- When regeneration of *P. nigra* in the gaps lags behind or is outcompeted by other species (e.g. *Betula pendula*) additional planting and removal of undesired species can be considered.
- Thinning should be focused on obtaining a mixed forest with a diverse forest structure, but should preserve a certain minimum amount of *P. nigra*, preferably in groups.

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