



Evidence of climate effects on the height-diameter relationships of tree species

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Abstract

• **Key message** The mean temperature from March to September affects the height-diameter relationship of many tree species in France. For most of these species, the temperature effect is nonlinear, which makes the identification of an optimal temperature possible. Increases in mean temperature could impact the volume supply of commercial species by the end of the twenty-first century.

• **Context** Height-diameter (HD) relationships are central in forestry since they are essential to estimate tree volume and biomass. Since the late 1960s, efforts have been made to generalize models of HD relationships through the inclusion of plot- and tree-level explanatory variables. In some recent studies, climate variables such as mean annual temperature and precipitation have been found to have a significant effect on HD allometry. However, in these studies, the effects were all considered to be linear or almost linear, which supposes that there is no optimal temperature and no optimal precipitation.

• **Aims** In this study, we tested the hypothesis that an optimum effect of temperature and precipitation exists on tree heights.

• **Methods** We fitted generalized models of HD relationships to 44 tree species distributed across France. To make sure that the climate variables would not hide some differences in terms of the local environment, the models included explanatory variables accounting for competition, tree social status and other plot-level factors such as slope inclination and the occurrence of harvesting in the last five years.

• **Results** It turned out that the temperature effect was significant for 33 out of 44 species and an optimum was found in 26 cases. The precipitation effect was linear and was found to be significant for only seven species. Although the two climate variables did not contribute as much as the competition and the social status indices to the model fit, they were still important contributors. Under the representative concentration pathway (RCP) 2.6 and the assumptions of constant form factors and forest conditions in terms of competition and social statuses, it is expected that approximately two thirds of the species with climate-sensitive HD relationships will generally be shorter. This would induce a decrease in volume ranging from 1 to 5% for most of these species.

• **Conclusion** Forest practitioners should be aware that the volume supply of some commercial species could decrease by the end of the twenty-first century. However, these losses could be partly compensated for by changes in the form factors and the species distributions.

Keywords Generalized height-diameter relationship · Mean temperature · Mean precipitation · Linear mixed-effects model · Climate change

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1 Introduction

Tree height is a critical variable in forestry because it is required for tree volume and biomass estimation, but its measurement is time-consuming. In most forest inventories, tree height is actually measured on a subsample of trees and not on all the trees in the sample plots. Traditionally, foresters have relied on height-diameter (HD) relationships in order to estimate missing heights. The idea consists of using the subsample of heights to fit a statistical model that relates tree height to its diameter, which is easier to measure. Using the HD relationship, unobserved heights

can be predicted and tree volume and biomass can then be estimated. The use of such HD relationships has proved to be convenient as it makes the estimation of volume and biomass possible, while limiting the investment in terms of resources and time.

Basic models of HD relationships can be fitted at the local scale, typically the forest stand. However, this means that a model fitted to a particular stand is subject to biases when used in another stand. Refitting models of HD relationships for each stand is tedious. Consequently, some authors have attempted to generalize these models since the late 1960s. The idea is to include additional tree- and plot-level explanatory variables in models of HD relationships so that they can adapt to different stand conditions.

Curtis (1967) was among the first who managed to fit such generalized HD relationships by including stand age in his model. Over the years, a large array of explanatory variables expressing the local conditions in terms of competition and fertility have been found to have a significant effect on HD relationships. Bégin and Raulier (1995) fitted HD relationships based on mean stand diameter and mean stand height. López Sánchez et al. (2003) used stand metrics such as site index, basal area, dominant diameter and dominant height. Using a mixed-model approach, Calama and Montero (2004) included stand density and dominant height in their model of HD relationships for stone pine (*Pinus pinea* L.).

Due to concerns related to climate change, the impact of climate variables on HD relationships has recently been studied. Changes in temperature and precipitation are likely to impact tree growth (Oliver and Larson 1996, p. 21). Because the impact on diameter growth might be different from that on height growth, this could affect HD relationships. Fortin et al. (2009) and Auger (2016) found a positive linear effect of the mean annual temperature on HD relationships in the province of Quebec, Canada. Hulshof et al. (2015) found a negative effect of temperature on the HD relationships of broadleaved species in the USA. In Spain, Lines et al. (2012) found a linear effect that was positive for some species but negative for others. In tropical forests, Feldpausch et al. (2011) fitted a general model of HD relationships that included mean annual temperature. Although the temperature effect was expressed through an exponential function in the model, its coefficient was so small that its actual representation was almost linear. In a few studies, mean annual precipitation was also found to affect HD relationships either positively or negatively depending on the species (e.g., Lines et al. 2012; Chave et al. 2015; Hulshof et al. 2015).

In all of the aforementioned studies, the effect of the climate variables was considered to be linear or nearly

linear. However, it can be reasonably assumed that these effects are nonlinear (Lines et al. 2012). The HD allometry is actually linked to carbon allocation. The physiological processes underlying this allocation are dependent on temperature and growth is known to reach a maximum at temperature between 20° and 35°C (Ericsson et al. 1996). Depending on the species, leaf net photosynthesis also show a maximum within the same range of temperature (Lin et al. 2012).

Likewise, optimal temperature and precipitation conditions that maximize tree heights for a given diameter must exist. Finding this optimum is not straightforward because the effect of climate variables can actually hide that of different forest structures if other explanatory variables are not accounted for in the model of HD relationships. To clearly assess the effect of the climate variables, it is good practice to also take other factors into account in these models, including competition, tree social status and other plot variables. This was precisely the objective of this study. Using the height observations of the French National Forest Inventory (NFI), we fitted models of HD relationships to 44 species. In addition to tree- and plot-level explanatory variables that accounted for the local environment, we tested the temperature and precipitation effects in these 44 models under the assumption that an optimum existed. Given the anticipated climate change, we also simulated what would be the impact on tree volume at the end of the twenty-first century if forest conditions remained the same.

2 Material and methods

2.1 Dataset

The data we used in this study were taken from the French NFI, which is under the responsibility of the National Geographical Institute (*Institut national de l'information géographique et forestière* (IGN)). The methodology behind the NFI is extensively described in IGN (2016). Since 2005, it follows a double-sampling scheme (Gregoire and Valentine 2008). A systematic grid covers the whole metropolitan territory with an annual sampling intensity of one point every 10 km². The grid is moved every year in order to maintain a systematic grid design after 5 and 10 years. For each point, the land use is first determined using aerial photographs. Each year, a subsample of the points that are located in forested areas is randomly selected for ground measurements. The field plots consist of three concentric fixed-area subplots in which the trees are measured according to their diameter at breast height (DBH, 1.3 m in height). Trees with DBH smaller than 22.5 cm but

Table 1 Mean diameter at breast height (DBH) and height for the 44 species to which the models of height-diameter relationships were fitted, where n is the number of trees

Species	n	DBH (cm)	Height (m)
<i>Abies alba</i> Mill.	31 807	33.1 (7.6, 134.3)	19.9 (2.4, 45.3)
<i>Acer campestre</i> L.	7473	17.2 (7.6, 75.8)	13.1 (2.2, 32.2)
<i>Acer monspessulanum</i> L.	1116	13.3 (7.6, 56.7)	8.5 (2.5, 20.8)
<i>Acer opalus</i> Mill.	1370	16.8 (7.6, 61.1)	11.1 (3.2, 25.4)
<i>Acer pseudoplatanus</i> L.	7416	22.4 (7.6, 106.3)	16.9 (2.2, 42.9)
<i>Alnus glutinosa</i> Gaertn.	5875	23.4 (7.6, 136.9)	17.2 (1.8, 38.4)
<i>Arbutus unedo</i> L.	1144	10.0 (7.6, 31.2)	6.1 (2.6, 12.5)
<i>Betula pendula</i> Roth.	16 139	18.5 (7.6, 69.4)	15.6 (1.9, 34.3)
<i>Carpinus betulus</i> L.	36 494	17.3 (7.6, 82.1)	15.1 (1.4, 36.8)
<i>Castanea sativa</i> Mill.	29 875	25.4 (7.6, 262.9)	15.1 (2.2, 38.3)
<i>Corylus avellana</i> L.	5935	9.2 (7.6, 30.2)	8.9 (1.4, 20.6)
<i>Crataegus monogyna</i> Jacq.	3416	10.3 (7.6, 39.5)	7.5 (2.0, 18.8)
<i>Fagus sylvatica</i> L.	57 733	30.3 (7.6, 174.1)	19.1 (1.6, 47.1)
<i>Fraxinus excelsior</i> L.	24 388	24.5 (7.6, 122.2)	18.6 (1.4, 44.5)
<i>Ilex aquifolium</i> L.	1311	11.0 (7.6, 60.5)	7.5 (2.2, 16.0)
<i>Larix decidua</i> Mill.	4154	33.9 (7.6, 179.2)	18.6 (3.1, 42.0)
<i>Picea abies</i> H. Karst	30 117	31.4 (7.6, 110.5)	20.7 (1.6, 46.5)
<i>Picea sitchensis</i> Carrière	2052	32.3 (7.6, 85.0)	20.3 (3.2, 39.1)
<i>Pinus halepensis</i> Mill.	4833	29.8 (7.6, 99.6)	12.5 (3.0, 29.6)
<i>Pinus nigra</i> R. Legay	5597	26.8 (7.6, 85.6)	14.1 (1.8, 35.2)
<i>Pinus nigra</i> var. <i>corsicana</i> Hyl.	5835	28.3 (7.6, 175.7)	15.9 (2.7, 44.1)
<i>Pinus pinaster</i> Aiton	22 511	32.5 (7.6, 123.2)	17.4 (2.5, 39.1)
<i>Pinus sylvestris</i> L.	35 343	28.6 (7.6, 93.6)	14.9 (1.4, 43.9)
<i>Pinus uncinata</i> Ramond ex DC.	2690	25.4 (7.6, 85.6)	10.5 (2.3, 24.9)
<i>Populus tremula</i> L.	7417	21.4 (7.6, 87.2)	18.1 (2.9, 40.0)
<i>Populus</i> spp.	1448	38.3 (7.6, 122.5)	24.9 (2.1, 48.0)
<i>Prunus avium</i> L.	7360	20.4 (7.6, 96.8)	14.9 (2.4, 37.9)
<i>Pseudotsuga menziesii</i> Franco	15 373	30.9 (7.6, 140.7)	22.1 (4.0, 48.0)
<i>Quercus ilex</i> L.	7657	16.4 (7.6, 198.9)	7.6 (1.7, 24.5)
<i>Quercus petraea</i> Liebl.	56 481	34.2 (7.6, 149.6)	20.1 (1.5, 43.1)
<i>Quercus pubescens</i> Willd.	29 460	20.6 (7.6, 192.3)	11.5 (1.8, 33.9)
<i>Quercus pyrenaica</i> Willd.	1769	24.8 (7.6, 96.4)	14.1 (2.5, 34.5)
<i>Quercus robur</i> L.	61 379	34.9 (7.6, 143.9)	18.8 (1.4, 43.0)
<i>Quercus rubra</i> L.	1477	24.5 (7.6, 119.4)	17.8 (4.5, 40.6)
<i>Quercus suber</i> L.	1674	30.7 (7.6, 117.8)	8.1 (2.2, 20.8)
<i>Robinia pseudoacacia</i> L.	8004	19.6 (7.6, 181.8)	16.1 (2.6, 37.6)
<i>Salix caprea</i> L.	4458	16.2 (7.6, 96.1)	11.0 (1.5, 32.0)
<i>Salix cinerea</i> L.	1085	16.8 (7.6, 96.8)	9.8 (2.0, 25.9)
<i>Sorbus aria</i> Crantz	3775	12.6 (7.6, 63.0)	10.0 (3.6, 26.0)
<i>Sorbus aucuparia</i> L.	1391	12.6 (7.6, 70.7)	10.1 (3.5, 29.6)
<i>Sorbus torminalis</i> Crantz	3281	13.0 (7.6, 53.5)	11.1 (3.5, 27.5)
<i>Tilia cordata</i> Mill.	2802	21.6 (7.6, 95.5)	16.0 (1.9, 35.5)
<i>Tilia platyphyllos</i> Scop.	2393	22.6 (7.6, 101.2)	15.9 (3.2, 37.1)
<i>Ulmus minor</i> Mill.	2862	13.4 (7.6, 79.6)	11.2 (2.7, 34.8)

The minimum and maximum of the variables appear in parentheses. *Populus* spp. includes all poplar species except *Populus tremula*

Table 2 Summary of the plot-level variables that were used to fit the models of height-diameter relationships, where n is the number of plots

Species	n	Stem density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Mean quadratic diameter (cm)	Slope (%)	Temperature (°C)	Precipitation (mm)
<i>Abies alba</i>	5638	789 (14, 3910)	34.6 (0.5, 110.6)	26.5 (8.2, 85.3)	33 (0, 200)	10.9 (4.8, 15.9)	708 (330, 1494)
<i>Acer campestre</i>	4168	1006 (14, 5740)	25.5 (0.5, 117.6)	19.7 (8.2, 60.8)	18 (0, 184)	13.2 (8.5, 16.6)	511 (315, 1133)
<i>Acer monspessulanum</i>	613	1117 (14, 4244)	17.7 (0.4, 53.4)	14.8 (7.6, 51.8)	27 (0, 120)	14.3 (8.8, 17.0)	490 (295, 843)
<i>Acer opalus</i>	713	1222 (33, 4067)	26.4 (0.4, 76.1)	17.4 (7.6, 58.1)	54 (0, 120)	12.0 (7.4, 15.6)	664 (364, 1153)
<i>Acer pseudoplatanus</i>	3076	813 (14, 5586)	27.6 (0.4, 110.6)	23.2 (7.6, 83.6)	24 (0, 200)	11.9 (3.4, 16.9)	601 (272, 1714)
<i>Alnus glutinosa</i>	1601	879 (14, 4322)	26.7 (0.4, 131.9)	21.6 (7.6, 70.7)	9 (0, 90)	13.4 (8.8, 17.8)	521 (293, 1196)
<i>Arbutus unedo</i>	582	1339 (88, 4391)	21.3 (0.4, 102.7)	14.8 (7.6, 44.7)	37 (0, 100)	15.6 (10.2, 18.5)	399 (186, 726)
<i>Betula pendula</i>	6161	905 (14, 5586)	24.6 (0.4, 99.2)	20.3 (7.6, 72.3)	13 (0, 196)	12.7 (4.5, 15.9)	505 (322, 1282)
<i>Carpinus betulus</i>	11 998	863 (14, 5586)	25.8 (0.4, 117.6)	22.1 (7.6, 86.0)	10 (0, 200)	13.2 (8.3, 16.1)	492 (324, 1145)
<i>Castanea sativa</i>	7857	933 (14, 5901)	28.7 (0.4, 129.3)	22.5 (7.6, 139.0)	21 (0, 185)	13.8 (9.0, 17.6)	506 (273, 1009)
<i>Corylus avellana</i>	3343	928 (88, 6254)	24.4 (0.4, 93.3)	19.3 (7.6, 50.9)	21 (0, 184)	12.9 (4.9, 17.0)	542 (288, 1302)
<i>Crataegus monogyna</i>	2107	906 (39, 4360)	23.6 (0.4, 129.3)	18.7 (7.6, 116.7)	17 (0, 190)	13.5 (9.0, 18.2)	497 (232, 1121)
<i>Fagus sylvatica</i>	14 152	737 (14, 5694)	28.8 (0.4, 112.7)	26.3 (7.6, 156.9)	26 (0, 200)	12.0 (4.7, 16.2)	600 (325, 1714)
<i>Fraxinus excelsior</i>	8175	859 (14, 4322)	25.7 (0.4, 117.6)	21.6 (7.6, 82.6)	21 (0, 200)	12.9 (6.7, 17.9)	545 (319, 1494)
<i>Ilex aquifolium</i>	797	936 (62, 3573)	31.8 (0.6, 88.9)	22.4 (8.5, 57.0)	26 (0, 174)	13.2 (7.9, 16.2)	547 (303, 1221)
<i>Larix decidua</i>	842	656 (14, 3331)	28.0 (0.4, 116.8)	26.5 (7.6, 76.7)	46 (0, 110)	9.1 (3.0, 15.1)	574 (355, 1142)
<i>Picea abies</i>	5627	819 (14, 4155)	34.4 (0.4, 121.0)	25.8 (7.6, 84.0)	28 (0, 111)	10.9 (3.4, 15.6)	728 (324, 1619)
<i>Picea sitchensis</i>	339	723 (14, 2741)	35.0 (1.7, 88.3)	27.8 (9.0, 57.2)	11 (0, 72)	12.4 (7.8, 14.7)	516 (326, 1002)
<i>Pinus halepensis</i>	1134	680 (14, 3565)	16.9 (0.4, 58.4)	20.5 (7.6, 69.0)	26 (0, 175)	16.1 (12.5, 18.5)	383 (186, 619)
<i>Pinus nigra</i>	1271	803 (14, 3890)	23.1 (0.4, 108.3)	20.5 (7.6, 68.8)	30 (0, 184)	12.9 (7.5, 17.0)	512 (342, 881)
<i>Pinus nigra</i> var. <i>corsicana</i>	1081	776 (14, 3173)	27.1 (0.4, 97.9)	23.6 (7.6, 130.5)	18 (0, 90)	13.2 (7.2, 16.3)	466 (303, 989)
<i>Pinus pinaster</i>	4379	653 (14, 4106)	23.4 (0.4, 130.8)	24.7 (7.6, 103.6)	9 (0, 130)	14.9 (9.8, 18.2)	456 (223, 784)
<i>Pinus sylvestris</i>	7891	798 (14, 3890)	25.9 (0.4, 108.3)	22.2 (7.6, 72.8)	25 (0, 200)	12.4 (4.5, 16.8)	512 (324, 1218)
<i>Pinus uncinata</i>	511	721 (14, 4002)	25.3 (0.5, 72.7)	23.1 (8.6, 59.5)	44 (0, 110)	7.7 (2.8, 13.0)	592 (399, 1279)
<i>Populus tremula</i>	2938	975 (14, 5586)	25.0 (0.4, 99.2)	19.7 (7.6, 66.2)	10 (0, 115)	13.2 (6.5, 17.1)	488 (319, 1714)
<i>Populus</i> spp.	526	833 (14, 3282)	25.4 (0.5, 100.4)	22.4 (8.6, 121.0)	3 (0, 50)	13.7 (10.8, 16.3)	430 (319, 740)
<i>Prunus avium</i>	4058	896 (14, 5586)	26.3 (0.5, 101.9)	21.3 (7.8, 74.4)	19 (0, 184)	13.2 (7.7, 16.9)	516 (332, 1714)
<i>Pseudotsuga menziesii</i>	2619	738 (14, 3590)	30.2 (0.5, 130.8)	25.2 (7.9, 66.3)	19 (0, 154)	12.6 (8.5, 16.1)	553 (324, 1179)
<i>Quercus ilex</i>	2979	1177 (14, 5040)	18.4 (0.4, 104.2)	14.8 (7.6, 70.7)	33 (0, 175)	15.3 (7.6, 18.4)	438 (189, 817)
<i>Quercus petraea</i>	13 779	759 (14, 5740)	25.7 (0.4, 104.2)	24.7 (7.6, 91.2)	14 (0, 200)	13.1 (7.5, 16.3)	489 (321, 1045)
<i>Quercus pubescens</i>	7765	960 (14, 4360)	19.9 (0.4, 104.2)	17.5 (7.6, 85.8)	28 (0, 175)	14.3 (7.4, 18.2)	480 (263, 1003)
<i>Quercus pyrenaica</i>	713	693 (14, 4106)	22.7 (0.5, 70.6)	23.6 (8.6, 81.8)	12 (0, 92)	14.8 (12.4, 16.2)	484 (324, 869)
<i>Quercus robur</i>	17 579	745 (14, 4322)	25.1 (0.4, 111.7)	24.2 (7.6, 110.3)	11 (0, 190)	13.6 (7.6, 17.8)	482 (298, 1139)
<i>Quercus rubra</i>	421	820 (14, 3119)	23.5 (0.6, 88.9)	21.0 (8.2, 56.5)	7 (0, 68)	13.7 (10.4, 16.1)	483 (326, 989)
<i>Quercus suber</i>	436	667 (14, 3820)	19.0 (0.5, 102.7)	22.3 (8.0, 69.8)	30 (0, 80)	16.7 (14.1, 18.5)	373 (202, 611)
<i>Robinia pseudoacacia</i>	2082	931 (28, 3814)	24.5 (0.4, 90.9)	19.6 (7.8, 59.0)	16 (0, 141)	14.1 (9.7, 18.1)	490 (323, 983)
<i>Salix caprea</i>	2293	998 (14, 5737)	21.3 (0.4, 117.6)	17.5 (7.6, 55.6)	15 (0, 177)	12.5 (5.6, 17.3)	524 (321, 1340)
<i>Salix cinerea</i>	502	839 (53, 4123)	19.7 (0.4, 73.3)	18.4 (7.6, 55.9)	10 (0, 84)	13.9 (5.5, 16.7)	557 (317, 949)
<i>Sorbus aria</i>	1969	1109 (39, 4597)	26.1 (0.4, 95.3)	18.2 (8.0, 52.2)	38 (0, 132)	11.8 (4.9, 16.3)	616 (369, 1397)
<i>Sorbus aucuparia</i>	705	953 (79, 3716)	29.2 (0.4, 116.8)	20.8 (8.0, 47.4)	36 (0, 106)	9.9 (3.4, 16.4)	733 (339, 1376)
<i>Sorbus torminalis</i>	1968	945 (39, 3291)	25.7 (0.4, 101.9)	20.2 (8.0, 54.8)	12 (0, 185)	13.9 (10.3, 16.1)	457 (324, 915)
<i>Tilia cordata</i>	1006	843 (26, 3910)	27.0 (1.0, 81.5)	23.3 (8.6, 86.9)	18 (0, 141)	13.1 (9.2, 17.1)	501 (297, 986)
<i>Tilia platyphyllos</i>	908	947 (14, 4597)	29.4 (1.7, 90.5)	22.4 (8.5, 72.6)	35 (0, 185)	12.6 (7.6, 16.5)	648 (325, 1161)
<i>Ulmus minor</i>	1387	938 (14, 3993)	23.6 (0.4, 89.9)	19.0 (7.6, 62.5)	12 (0, 85)	14.0 (9.6, 17.9)	443 (239, 885)

The range of the variables appears in parentheses. Stem densities, mean quadratic diameters, and basal areas include all species in the plots. Temperatures and precipitations are the 1961–1990 averages between the months of March and September. *Populus* spp. includes all poplar species except *Populus tremula*

greater than or equal to 7.5 cm are measured on a radius of 6 m from the plot center. Trees with DBH greater than or equal to 22.5 cm but smaller than 37.5 cm are measured on a 9-m-radius subplot. Finally, trees with DBH greater than or equal to 37.5 cm are measured on a radius of 15 m from the plot center. For each tree, the circumference at breast height was measured to the nearest centimeter. The DBH was calculated by dividing the circumference by the constant π under the assumption that the cross section at 1.3 m in height is perfectly circular.

Until 2008, the heights of all the trees located in the field plots were measured. In 2009, a simplification of the sampling procedure was undertaken and about 75% of the heights were measured. We gathered all the height measurements that were available from 2005 to 2015 in order to create the dataset we used in this study for a total of 592 400 observed heights.

The dataset included more than 150 different tree species with many of them being marginal. We discarded all the species that had less than 1000 observations in the dataset, which left 44 species. This screening left a total of 566 170 height observations distributed in 65 420 plots. It is worth mentioning that poplar species were not distinguished during the inventory, except for *Populus tremula* L. All other species of poplar were grouped under the label *Populus* spp. A summary of the dataset can be found in Tables 1 and 2.

In addition to tree metrics, the inventory protocol included the measurement of many plot-level variables such as slope inclination, soil texture, composition and depth, as well as a vegetation survey. The occurrence of natural and anthropogenic disturbances in the past five years was also recorded. Natural disturbances included fires, windstorms and droughts. The occurrence of anthropogenic disturbance, namely harvesting, was recorded when stumps could be observed within a 0.2-ha area around the plot center. For both natural and anthropogenic disturbances, the inventory protocol specified a class variable based on the severity of the disturbance. However, the number of observations in each class was largely unbalanced in both cases, which could be a statistical issue. In order to facilitate the statistical analysis, we grouped the different classes into two categories: occurrence and non-occurrence.

As a complement to these tree- and plot-level variables, we retrieved climate variables from existing national climate maps that were generated in the context of another study (Piedallu et al. 2013). These maps provide monthly mean temperatures and precipitations as well as soil water balance and evapotranspiration at a 1-km² resolution for the 1961–1990 period. The climate variables were modeled using uninterrupted series provided by a set of 237 and 432 meteorological stations for temperatures and precipitations, respectively. The explanatory variables in these models

were variables describing topography, solar radiation, land use, and distances to the seas. The evaluation of these maps against independent datasets proved to be satisfactory. The reader is referred to Piedallu et al. (2013) for further details about the methodology.

2.2 Statistical model

The model we used in this study was inspired by Fortin et al. (2009). It relies on the following basic linear model:

$$h_{ij} = 1.3 + A_{ij} \ln(\text{DBH}_{ij} + 1) + B_{ij} \ln^2(\text{DBH}_{ij} + 1) + \epsilon_{ij} \quad (1)$$

where h_{ij} is the height (m) of tree j in plot i , DBH_{ij} is the diameter at breast height (1.3 m in height), A_{ij} and B_{ij} are the parameters of the model and ϵ_{ij} is the residual error term, which is assumed to be normally distributed with mean 0 and variance σ_{res}^2 , i.e., $\epsilon_{ij} \sim N(0, \sigma_{\text{res}}^2)$. Although it is linear, this model exhibits a nearly asymptotic pattern like most common nonlinear models of HD relationships. The reader can find many of these common nonlinear models in López Sánchez et al. (2003).

A generalized model is obtained by substituting linear functions of plot- and tree-level explanatory variables for A_{ij} and B_{ij} in Eq. 1 (Mehtätalo et al. 2015). The term “generalized model” refers to the inclusion of additional explanatory variables in the model, which makes the HD relationships generalizable over large areas rather than having to fit individual relationships to different stands (Temesgen and von Gadow 2004). This term is not to be confused with generalized linear models used in statistics to model non-Gaussian responses (see McCullagh and Nelder 1989).

Even if a model accounts for many plot-level variables, the possibility still exists that some of them have been omitted (Gregoire 1987). The combined effect of these omitted variables can be represented as a plot random effect, which leads to a mixed-effects (both random and fixed) model. Gregoire (1987) and Lappi and Bailey (1988) are among the first who used this approach in forestry. It is widely used today and, consequently, it will only be briefly described here within the aforementioned context. For further details and a broader perspective of this approach, the reader is referred to Pinheiro and Bates (2000).

The model shown in Eq. 1 can be converted into a mixed model by adding a plot random effect as follows:

$$h_{ij} = 1.3 + (A_{ij} + b_i) \ln(\text{DBH}_{ij} + 1) + B_{ij} \ln^2(\text{DBH}_{ij} + 1) + \epsilon_{ij} \quad (2)$$

where b_i is a random effect associated with plot i , which is assumed to be normally distributed with mean 0 and variance σ_{plot}^2 , i.e. $b_i \sim N(0, \sigma_{\text{plot}}^2)$.

The model in Eq. 2 has two error terms, one at plot level and one at tree level. Consequently, the variance of h_{ij} has two components:

$$\mathbb{V}(h_{ij} | \mathbf{x}_{ij}) = \sigma_{\text{res}}^2 + \sigma_{\text{plot}}^2 \ln^2(\text{DBH}_{ij} + 1) \quad (3)$$

where \mathbf{x}_{ij} is a row vector containing the explanatory variables of the model. An interesting feature of such a mixed-model approach is that it makes it possible to distinguish the variance that stems from the unobserved plot factors, i.e. $\sigma_{\text{plot}}^2 \ln^2(\text{DBH}_{ij} + 1)$, from that of the tree-level

Table 3 Explanatory variables included in the functions that replaced parameters A_{ij} and B_{ij} in the mixed model

Species	Basal area of other trees	Social status	Slope inclination	Harvest occurrence	Temperature	Precipitation
<i>Abies alba</i>	○	●	○	○	●	○
<i>Acer campestre</i>	○	○	○		●	
<i>Acer monspessulanum</i>	○		○		●	
<i>Acer opalus</i>	○	○	○		○	○
<i>Acer pseudoplatanus</i>	○	○	○		●	
<i>Alnus glutinosa</i>	○	●	○	○	●	
<i>Arbutus unedo</i>	○					
<i>Betula pendula</i>	○	●	○	○	●	
<i>Carpinus betulus</i>	○	●	○	○	●	
<i>Castanea sativa</i>	○	○	○		●	
<i>Corylus avellana</i>	○		○		●	
<i>Crataegus monogyna</i>	○	●	○			
<i>Fagus sylvatica</i>	○	●	○	○	●	○
<i>Fraxinus excelsior</i>	○	○	○	○	●	
<i>Ilex aquifolium</i>						
<i>Larix decidua</i>	○	○		○	○	
<i>Picea abies</i>	○	●	○	○	●	
<i>Picea sitchensis</i>	○	○		○		
<i>Pinus halepensis</i>	○				●	
<i>Pinus nigra</i>	○	●	○	○	●	
<i>Pinus nigra var. corsicana</i>	○	○	○	○	○	
<i>Pinus pinaster</i>	○	●	○	○	●	○
<i>Pinus sylvestris</i>	○	○	○	○	●	
<i>Pinus uncinata</i>	○	●		○	○	
<i>Populus tremula</i>	○	○	○	○	●	
<i>Populus spp.</i>	○	○				
<i>Prunus avium</i>	○	○	○	○	●	
<i>Pseudotsuga menziesii</i>	○	●		○	●	
<i>Quercus ilex</i>	○	○				○
<i>Quercus patraea</i>	○	●	○	○	●	
<i>Quercus pubescens</i>	○	○	○	○	●	
<i>Quercus pyrenaica</i>	○	●			●	
<i>Quercus robur</i>	○	○	○	○	●	
<i>Quercus rubra</i>	○	○				
<i>Quercus suber</i>	○		○	○	○	○
<i>Robinia pseudoacacia</i>	○	○	○		●	
<i>Salix caprea</i>	○			○	●	
<i>Salix cinerea</i>	○					
<i>Sorbus aria</i>	○	○	○	○	●	
<i>Sorbus aucuparia</i>	○		○	○	○	

Table 3 (continued)

Species	Basal area of other trees	Social status	Slope inclination	Harvest occurrence	Temperature	Precipitation
<i>Sorbus torminalis</i>	○		○	○		○
<i>Tilia cordata</i>	○	●	○			
<i>Tilia platyphyllos</i>	○	○	○			
<i>Ulmus minor</i>	○	●	○		○	
Total	43 / 0	19 / 15	31 / 0	25 / 0	7 / 26	7 / 0

Circles (○) and dots (●) indicate that the effect was entered into the model into a linear or quadratic fashion, respectively. The totals indicate the number of linear effects over the number of quadratic effects. *Populus* spp. includes all poplar species except *Populus tremula*

residual errors, i.e. σ_{res}^2 . On the basis of Eq. 3, it is clear that term $\sigma_{\text{plot}}^2 \ln^2(\text{DBH}_{ij} + 1)$ increases along with tree DBH, indicating that the contribution of the plot random effect to the total variance of the prediction error increases as well. Consequently, a DBH exists for which the plot random effect and the residual error contribute equally to the variance of the prediction error, i.e.

$$\exists! \text{DBH} : \sigma_{\text{plot}}^2 \ln^2(\text{DBH} + 1) = \sigma_{\text{res}}^2 \quad (4)$$

Beyond this threshold, the plot random effect contributes more than the residual error and *vice versa*. This DBH, hereafter referred to as the DBH for variance parity ($\text{DBH}_{\text{parity}}$), can be estimated from Eq. 4 as:

$$\widehat{\text{DBH}}_{\text{parity}} = e^{\sqrt{\frac{\sigma_{\text{res}}^2}{\sigma_{\text{plot}}^2}} - 1} \quad (5)$$

where the hat denotes estimated parameters.

2.3 Model specifications and goodness of fit

The models included tree- and plot-level explanatory variables in order to account for the local environment of the trees. At the tree level, competition is known to impact HD relationships (López Sánchez et al. 2003; Calama and Montero 2004) since trees tend to be slender when they grow in dense stands. We retained plot basal area as a competition index, but we then modified this variable by subtracting the basal area of the subject tree. The reason behind this was that a given tree would not exert any competition on itself. For the sake of simplicity, we will refer to this variable as the basal area of other trees.

In addition to competition, it could be assumed that the social status had an influence over the HD relationships. For the same basal area, dominated trees tend to be more slender in general than dominant trees (Pretzsch 2009, p. 189). We tested a social status index, which was calculated as the ratio between the DBH of the subject tree and the plot mean quadratic diameter.

Regarding the plot-level explanatory variables, slope inclination was considered to be a proxy for drainage since water runs off faster when the slope is steep. The occurrence of harvesting was also included in the model since it clearly modified the effect of competition. For two plots with the same basal area, trees should be more slender in the one that was just harvested because the competition level was higher before harvesting.

After testing these tree- and plot-level explanatory variables, we integrated the climate variables in the models. More precisely, we tested the mean temperature and mean precipitation between March and September over the 1961–1990 period.

All the aforementioned explanatory variables were tested in the mixed-effects model shown in Eq. 2 in the following order: basal area of other trees, social status index, slope inclination, occurrence of harvesting, mean temperature, and mean precipitation. The model was fitted for each species independently, resulting in 44 fits. A particular explanatory variable was kept in the model only if its effect was significant and if it improved the model likelihood, as indicated by the Akaike and Bayesian information criteria (AIC and BIC, see Pinheiro and Bates 2000, p. 84). As suggested by Burnham and Anderson (2002, p. 70) we considered a decrease of 2 units in AIC and BIC as the minimal improvement to keep the explanatory variable in the model.

When testing a particular explanatory variable, it was first included in a linear fashion in the function that replaced parameter A_{ij} . In the case of lack of fit, two options were successively tested. The first consisted of adding the explanatory variable in a linear fashion in the function that replaced parameter B_{ij} . The second was the specification of the square of the explanatory variable in addition to the linear term in the function that replaced parameter A_{ij} .

After testing each variable, we checked whether the normalized residuals (Pinheiro and Bates 2000, p. 239) were normally distributed with homogeneous variances. As suggested in Fortin et al. (2008), an empirical Pearson correlation coefficient was calculated to check if the plot random effect associated with parameter A_{ij} properly

accounted for the covariance between the within-plot residual error terms. Normalized residuals were also plotted against the explanatory variable that was just tested to make sure there was no unaccounted for trend left in the models.

All the fits and analyses were carried out using the MIXED procedure available in SAS (Littell et al. 2006). A cross-validation was also carried out in order to test the performance of the 44 models. We performed an 11-fold

Table 4 Ranking of the explanatory variables in terms of AIC change and anticipated volume change ($\widehat{\Delta v}$) if temperatures increased by 1.5°C compared to the 1961–1990 period

Species	Basal area of other trees	Social status	Slope inclination	Harvest occurrence	Temp.	Prec.	$\widehat{\Delta v}$
<i>Abies alba</i>	3	1	5	4	2	6	+ 4.5%
<i>Acer campestre</i>	4	1	2		3		− 5.5%
<i>Acer monspessulanum</i>	1		2		3		− 3.8%
<i>Acer opalus</i>	2	4	5		3	1	+ 5.9%
<i>Acer pseudoplatanus</i>	2	1	4		3		+ 0.4%
<i>Alnus glutinosa</i>	2	1	4	5	3		− 2.9%
<i>Arbutus unedo</i>	1						
<i>Betula pendula</i>	1	2	3	5	4		− 0.3%
<i>Carpinus betulus</i>	3	1	2	5	4		− 1.3%
<i>Castanea sativa</i>	2	1	3		4		− 6.9%
<i>Corylus avellana</i>	3		2		1		+ 2.1%
<i>Crataegus monogyna</i>	3	1	2				
<i>Fagus sylvatica</i>	3	1	4	6	2	5	+ 4.3%
<i>Fraxinus excelsior</i>	2	1	3	5	4		− 2.2%
<i>Ilex aquifolium</i>							
<i>Larix decidua</i>	2	1		4	3		+ 5.2%
<i>Picea abies</i>	3	1	5	4	2		+ 4.0%
<i>Picea sitchensis</i>	1	2		3			
<i>Pinus halepensis</i>	1				2		− 0.7%
<i>Pinus nigra</i>	1	2	5	4	3		− 0.8%
<i>Pinus nigra</i> var. <i>corsicana</i>	1	2	5	4	3		+ 3.3%
<i>Pinus pinaster</i>	2	1	3	6	4	5	− 4.9%
<i>Pinus sylvestris</i>	1	2	3	5	4		+ 2.6%
<i>Pinus uncinata</i>	1	2		4	3		+ 7.5%
<i>Populus tremula</i>	2	1	3	5	4		− 2.9%
<i>Populus</i> spp.	1	2					
<i>Prunus avium</i>	2	1	3	5	4		− 3.8%
<i>Pseudotsuga menziesii</i>	2	1		4	3		− 0.5%
<i>Quercus ilex</i>	1	2				3	0.0%
<i>Quercus patraea</i>	2	1	3	5	4		− 1.2%
<i>Quercus pubescens</i>	1	2	3	5	4		− 4.0%
<i>Quercus pyrenaica</i>	1	3			2		− 22.2%
<i>Quercus robur</i>	2	1	3	5	4		− 3.1%
<i>Quercus rubra</i>	1	2					
<i>Quercus suber</i>	1		2	3	4	5	− 4.4%
<i>Robinia pseudoacacia</i>	2	1	3		4		− 3.7%
<i>Salix caprea</i>	1			3	2		− 4.8%
<i>Salix cinerea</i>	1						
<i>Sorbus aria</i>	2	3	1	5	4		− 0.1%
<i>Sorbus aucuparia</i>	1		4	3	2		+ 3.7%
<i>Sorbus torminalis</i>	1		2	4		3	0.0%

Table 4 (continued)

Species	Basal area of other trees	Social status	Slope inclination	Harvest occurrence	Temp.	Prec.	$\widehat{\Delta v}$
<i>Tilia cordata</i>	2	1	3				
<i>Tilia platyphyllos</i>	2	1	3				
<i>Ulmus minor</i>	3	1	4		2		− 4.3%
Total	35	31	8	0	9	1	

Temp.: mean temperature

Prec.: mean precipitation. A ranking of 1 indicates the greatest contribution in terms of AIC decrease. The totals indicate the number of times the explanatory variable ranked first or second. *Populus* spp. includes all poplar species except *Populus tremula*

cross-validation in which the data for a particular year were successively omitted in the model and then used as an independent dataset for testing model predictions in terms of biases and root mean square errors.

When the final models were obtained, we refitted them and successively omitted the effects one by one in order to assess their contribution to the model fit. Larger differences in AIC between the simplified model and the final model were interpreted as greater contributions to the model fit. We therefore ranked the different effects and checked if there were emerging patterns across species.

2.4 Impact of climate variables on tree volume

Once the models were fitted, they could be used to anticipate the effect climate change would have on tree volume. Tree volume (v_{ij}) can be estimated as:

$$\hat{v}_{ij} = c \cdot \pi \cdot \text{DBH}_{ij}^2 \hat{h}_{ij} \quad (6)$$

where c is the form factor (Pretzsch 2009, p. 199) and \hat{h}_{ij} is the height prediction for tree j in plot i based on the fixed effects only. If we assume that the forest conditions remain the same and the form factor remains constant, then the average relative change in volume (Δv) can be estimated as:

$$\widehat{\Delta v} = \frac{\sum_i \sum_j w_{ij} \cdot \text{DBH}_{ij}^2 \hat{h}_{ij}^*}{\sum_i \sum_j w_{ij} \cdot \text{DBH}_{ij}^2 \hat{h}_{ij}} - 1 \quad (7)$$

where w_{ij} is the sampling weight of tree j in plot i and \hat{h}_{ij}^* is the height prediction under the anticipated climate change. Note that form factor c and constant π have been factored out and sampling weight w_{ij} needs to be included in Eq. 7 because the plot area changes depending on tree DBH.

In terms of anticipated climate change, we used the representative concentration pathway (RCP) 2.6 of the IPCC, which is in line with the Paris climate agreement (Sanderson et al. 2016). RCP 2.6 is based on the forecasts of 32 models (IPCC 2013a, p. 1315). Compared to the 1986–2005 reference period, it predicts that summer temperatures

will be 1.0 to 1.5°C higher in 2081–2100 in France, while summer precipitation is expected to remain stable (IPCC 2013b, p. 75). For the sake of simplicity, we assumed that the temperature from March to September would increase by 1.5°C compared to the 1961–1990 period and that all other explanatory variables would keep their current values.

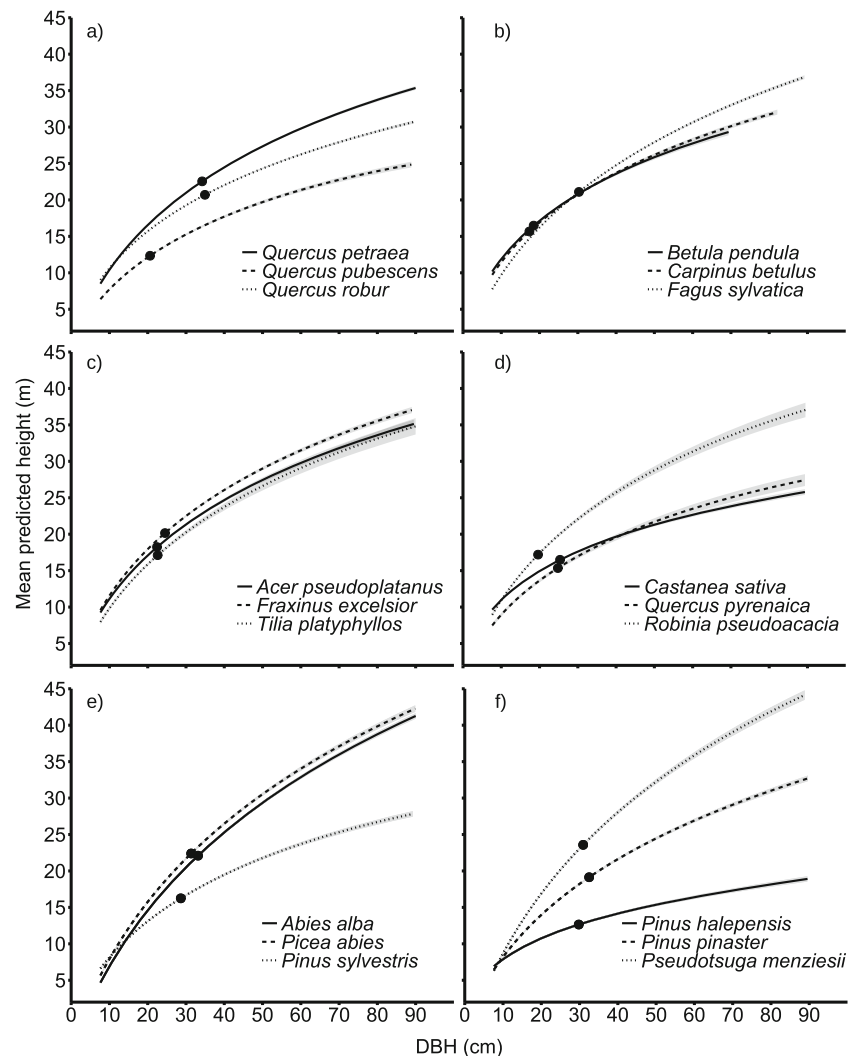
3 Results

The summary of the explanatory variables that had a significant effect on tree height is given in Table 3. The basal area of other trees was entered into all of the models, except that of *Ilex aquifolium*, in a linear manner. The social status index was entered into the model for 34 out of 44 species, half of these being in a quadratic fashion. The mean temperature was part of 33 models, with the quadratic form being more frequent than the linear form. The slope came next, being part of 31 out of 44 models, all in the linear form. The harvest occurrence also had a significant effect in 25 models. Finally, the mean precipitation was kept in seven models. The parameter estimates are listed in the Supplementary Material (Tables SM1 and SM2).

The cross-validation showed estimated biases that were generally within the range of $\pm 4\%$ and root mean square errors below 30% (see Tables SM3 and SM4 in the Supplementary Material). There was no evidence of lack of fit as those biases that exceeded the range $\pm 4\%$ could not be associated with any species in particular. However, year 2005 was the one that counted more estimated biases out of the $\pm 4\%$ range.

The ranking of the different variables in terms of their contribution to the model fit is shown in Table 4. The basal area of the other trees and the social status index accounted for the most or the second most important effect in 35 and 31 models, respectively. The slope inclination came next with eight out of 44 models, followed by the temperature with nine models. The precipitation counted among the two most important effects in only one model.

Fig. 1 Mean predicted heights as a function of tree diameter at breast height (DBH). Gray areas delineate the 95% confidence intervals. The dots indicate the average DBH in the dataset. The average, as observed in the dataset, was used for the other model variables, except for the mean quadratic diameter that was set to the DBH in order to maintain a constant social status



For most species, the DBH for variance parity was smaller than 20 cm (see SM5 in the Supplementary Material). In other words, beyond this threshold the plot random effect contributed more than the residual error to the variance of the predictions. *Abies alba*, *Larix decidua* and *Picea abies* were the only species that exceeded this threshold, with DBH for variance parity estimated at 26.6 cm, 20.4 cm, and 21.0 cm, respectively.

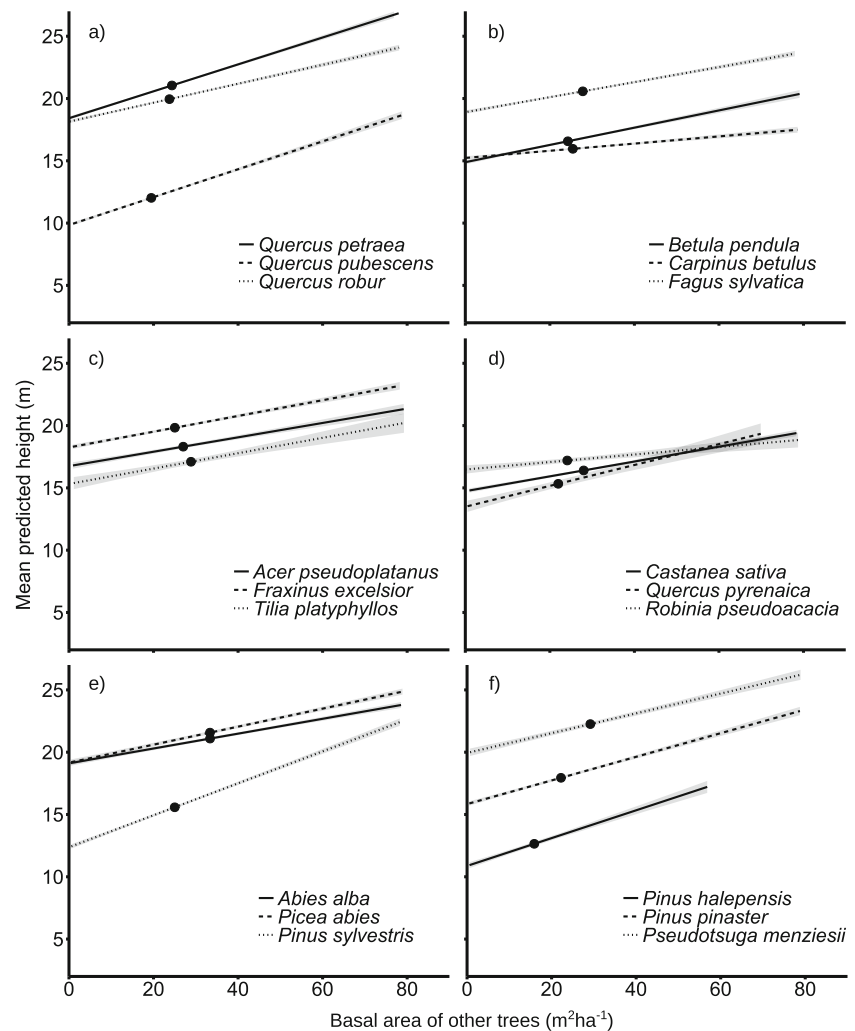
In order to better determine the magnitude of the different effects, model predictions were generated. Mean predicted heights as a function of tree DBH are shown in Fig. 1 for the most abundant species in terms of volume (IGN 2017). Predictions were generated by varying tree DBH while maintaining the other model variables at their average values in the dataset. The mean quadratic diameter was the only exception to this rule. It was set to the DBH to ensure that the social status of the tree would not change. For the same DBH, mediterranean and sub-Mediterranean

species generally tended to be shorter than the other species. This was the case of *Quercus pubescens*, *Castanea sativa*, *Quercus pyrenaica*, and *Pinus halepensis* (Fig. 1a, d, and f). Coniferous species such as *Abies alba*, *Picea abies*, and *Pseudotsuga menziesii* generally tended to be taller than broadleaved species for a given DBH (Fig. 1e, f).

The effect of the basal area of other trees, which represents the competition at the plot level, is shown in Fig. 2 for the average trees of the most common species. All other things considered, an increase in the basal area of other trees induced an increase in tree height for all species. Some species were less sensitive than others, such as *Carpinus betulus* and *Robinia pseudoacacia* (Fig. 2b, d). In contrast, *Pinus sylvestris* appeared to be one of the most sensitive species to the basal area of other trees.

The effect of the social status on tree height is shown in Fig. 3. All other things considered, dominant trees, i.e., trees with social status indices greater than 1, were more

Fig. 2 Mean predicted heights as a function of the basal area of other trees. Gray areas delineate the 95% confidence intervals. The dots indicate the average basal area of other trees in the dataset. The average, as observed in the dataset, was used for the other model variables



tapered while dominated trees, as indicated by social status indices smaller than 1, tended to be more slender. Some species were less sensitive to social status than others. For example, *Castanea sativa* and *Quercus pyrenaica* showed small, but still significant, differences between dominant and dominated trees (Fig. 3d).

The slope inclination had a negative effect on the height of most species (Fig. 4). *Abies alba* and *Picea abies* were the only notable exceptions with a slight increase in tree height along the slope inclination. The effect of harvest occurrence was positive in all the models where it was entered and generally corrected for the decrease in basal area following thinning (result not shown).

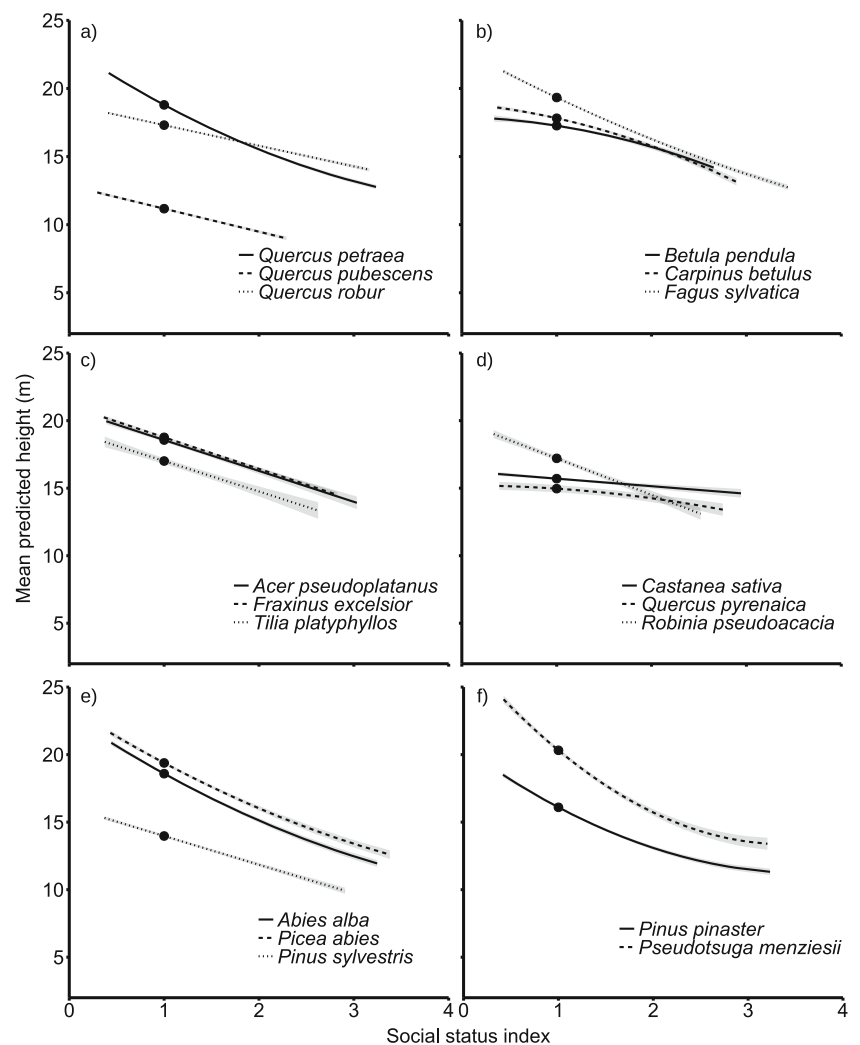
The effect of mean temperature from March to September over the 1961–1990 period is shown in Fig. 5 for the major species with a quadratic effect. All other things considered, a change in the temperature could induce changes of several meters in the mean predicted heights. For most species, the observed average temperatures in the dataset were close to the temperature that maximized tree heights.

The exceptions to this pattern were *Fagus sylvatica*, *Abies alba* and *Picea abies* for which the current average temperature was below the optimal temperature (Fig. 5b,e), and *Castanea sativa* for which the current average temperature was beyond the optimal temperature (Fig. 5d).

The precipitation effect was positive (Fig. 6). Some species were less sensitive than others to changes in precipitation. For example, *Abies alba* seemed less affected than *Pinus pinaster*, *Quercus suber*, and *Fagus sylvatica*.

As shown in Table 4, the anticipated volume change at the end of the twenty-first century under the RCP 2.6 climate change scenario and the assumptions of constant forest conditions and constant form factors varied across species. A total of 22 species showed a decrease in volume, most of them being considered either as Mediterranean species or as species typical of plains and hills (Rameau et al. 1989). The species with the greatest decrease in volume was *Quercus pyrenaica*, followed by *Castanea sativa* and *Acer campestre*, with estimated changes of -22.2% , -6.9% , and -5.5% , respectively. An increase in

Fig. 3 Mean predicted heights as a function of social status index calculated as the ratio between tree DBH and plot mean quadratic diameter. Positive and negative indices indicate dominant and dominated trees, respectively. Gray areas delineate the 95% confidence intervals. The dots indicate that the social status index is equal to 1, i.e., tree DBH is equal to mean quadratic diameter. The average, as observed in the dataset, was used for the other model variables



tree volume was predicted for 11 species that were mainly considered as typical of mountain areas. *Pinus uncinata*, *Larix decidua*, *Abies alba*, and *Fagus sylvatica* counted among the species with the greatest increases, estimated at + 7.5%, + 5.2%, + 4.5% and + 4.3%, respectively. When pooling the 44 species together, the models predicted a decrease of 0.3%.

4 Discussion

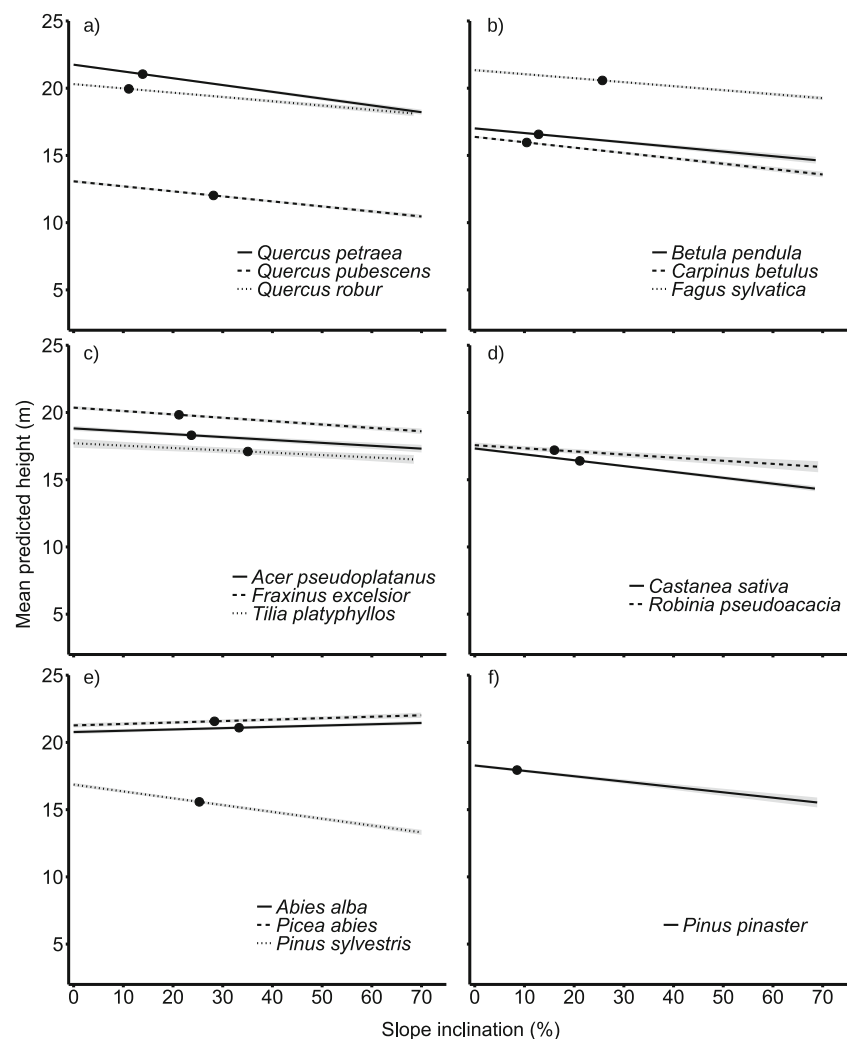
The existing literature provides a large array of plot metrics that have been tested in HD relationship models, including stem density, basal area, dominant height, or diameter, arithmetic or quadratic mean diameter, relative spacing indices, and age (Castedo Dorado et al. 2006; Garber et al. 2009; Crecente Campo et al. 2014; Mehtätalo et al. 2015; Sharma and Breidenbach 2015; Adamec and Drápela 2016; Saud et al. 2016). However, climate variables have been

overlooked in most studies. With the concerns related to climate change, evaluating the climate effects in generalized HD relationships has become essential, especially if those relationships are to be used in growth forecasts. Given that climate variables are now available through maps or software (e.g., Régnière et al. 2014)), we hardly see any reason for not testing them in these HD relationship models. Compared with previous studies, the originality of our work lies in the fact that our HD relationship models accounted for temperature and precipitation in addition to tree competition, tree social status, and plot-level factors.

4.1 Temperature and precipitation effects

Our results show that the mean temperature from March to September had a significant effect on the height of most species, with this effect being quadratic in most cases (Table 3). This effect could hardly be explained by different forest conditions since the models already accounted for tree

Fig. 4 Mean predicted heights as a function of the slope inclination. Gray areas delineate the 95% confidence intervals. The dots indicate the average slope inclination in the dataset. The average, as observed in the dataset, was used for the other model variables



size and social status, competition, slope inclination, and the occurrence of harvesting. Moreover, the magnitude of the effect was considerable, showing that the mean predicted height can change by several meters depending on the mean temperature (Fig. 5). We found either no significant effect or only a linear effect of the temperature for many species with less than 1000 plots, which suggests that the sample size and the geographical scope are two critical factors to capture this effect.

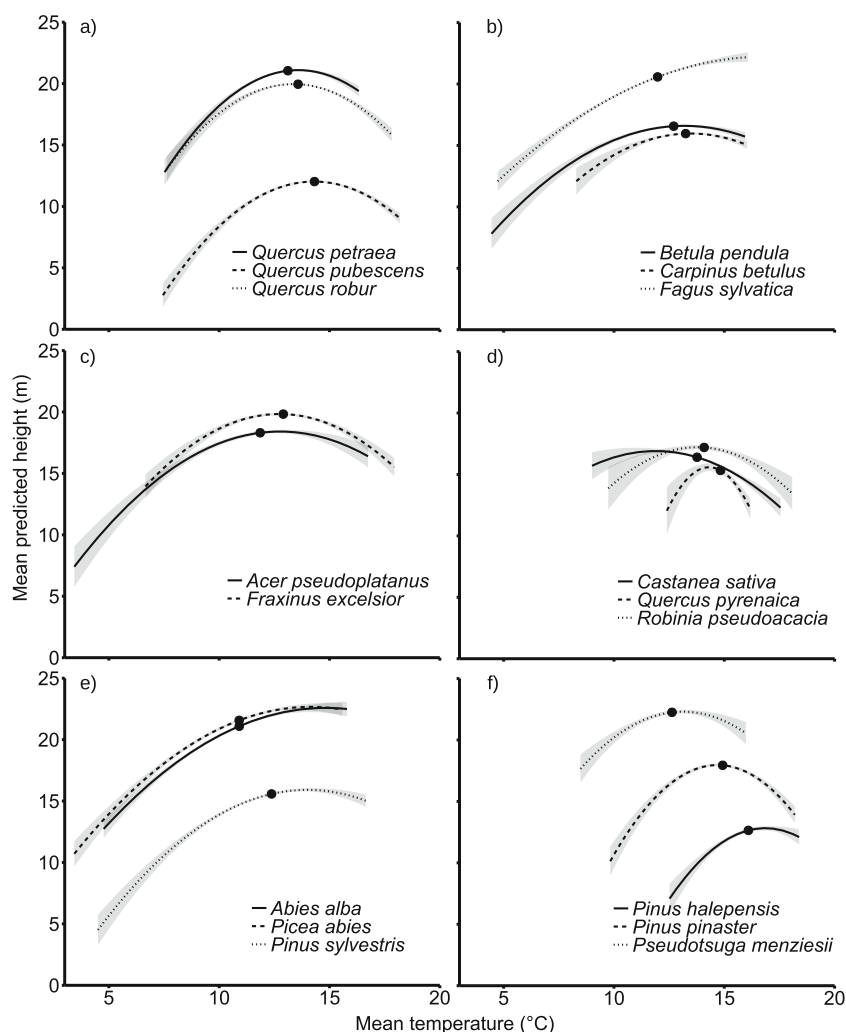
The results we obtained about temperature are in accordance with those of previous studies. First, an optimal temperature exists for photosynthesis and growth (Ericsson et al. 1996; Lin et al. 2012). Secondly, temperature affects height growth more than diameter growth (Way and Oren 2010). The predicted heights shown in Fig. 5 reflect these two aforementioned trends: at the optimal temperature, trees grow faster and they allocate the additional carbon to height growth in priority.

A quadratic effect of temperature like the one we found for 26 out of 44 species also supports the idea of a thermal

optimum for height growth (Way and Oren 2010). From an ecological perspective, the temperature of the growing season clearly contributes to the definition of the thermal niche of a particular species. It was surprising to find that the average temperatures observed in the dataset were close to the optimal temperatures for most species, as shown in Fig. 5. In other words, the trees of a particular species are more likely to be found in areas where the temperature effect on their heights is optimal. The optimal occurrence of plant species has already been found to coincide with other optimal features such as abundance (Van Couwenberghe et al. 2013). This assertion seems logical, but considering that nearly half the French forest is intensively managed (Anonymous 2000), it can be further concluded that either forest management has not greatly impacted the distribution of most tree species or that it has favored the establishment of these species under optimal conditions.

Site indices have traditionally been used as a proxy for site fertility in models of HD relationships (e.g., López Sánchez et al. 2003). However, some authors recently

Fig. 5 Mean predicted heights as a function of the 1961–1990 mean temperature from March to September. Gray areas delineate the 95% confidence intervals. The dots indicate the average temperature in the dataset. The average, as observed in the dataset, was used for the other model variables



demonstrated that site index was not as stable over time as was expected (Bontemps et al. 2009). As a response, climate-sensitive site indices were developed (e.g., Seynave et al. 2005). Whether they are climate sensitive or not, site indices are never truly observed, but are predicted instead. From a statistical point of view, integrating them in a model of HD relationships makes uncertainty assessment of predictions more complex. For this reason, it seemed preferable to include these climate variables directly in the models of HD relationships and not through a climate-sensitive site index.

The identification of these optimal temperatures and the fact that the average observed temperatures were close to them can be a concern in the context of climate change. Under the representative concentration pathway (RCP) 2.6 of the IPCC, summer temperatures are expected to increase by 1.5°C by the end of the twenty-first century in France (IPCC 2013b, p. 75). This increase complies with the target of the Paris climate agreement (UNFCCC 2015). As shown in Table 4, this change in temperature is likely to affect

tree height, which in turn impacts tree volume. Under the assumption that forest conditions, in terms of competition and social status, remain the same and that the form factor is constant, approximately two thirds of the species with climate-sensitive HD relationships showed decreases in volume. For some of these species, the decrease was close to or even greater than 5% (Table 4). It must be stressed that the assumptions behind these anticipated changes are strong. First, forest conditions will probably be different at the end of the twenty-first century. Actually, the decrease in volume could be compensated for if the distribution of the species shifted towards sites that are currently colder than the optimum. It has been suggested that migration-assisted strategies could be an effective means of mitigation against climate change (Hof et al. 2017).

Secondly, the taper of some species was recently found to be climate sensitive (Schneider et al. 2018), which means that the form factor will probably change in the future. Species with greater tolerance to shade and waterlogging tend to decrease their taper and, consequently, to increase

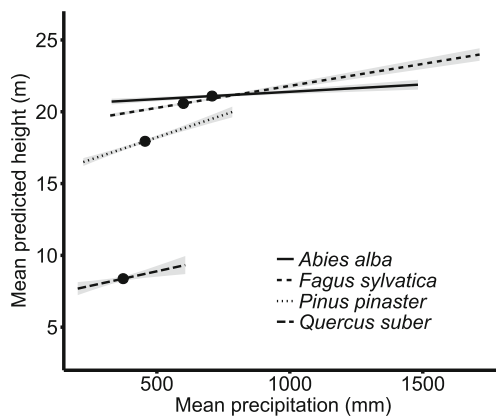


Fig. 6 Mean predicted heights as a function of the 1961–1990 mean precipitation from March to September. Gray areas delineate the 95% confidence intervals. The dots indicate the average precipitation in the dataset. The average, as observed in the dataset, was used for the other model variables

their volume for the same DBH and height (Schneider et al. 2018). Depending on the species ecology, this taper adaptation could either exacerbate or compensate the change in volume that we found in this study. Because they rely on these two strong assumptions, the anticipated volume changes shown in Table 4 should be considered with precaution. The true change should lie somewhere between these predicted changes and no change at all, which means perfect adaptation. This remains to be investigated.

In order to identify this optimal temperature, the territory under study must show a diversity of temperatures and these temperatures must include the optimal temperature of the thermal niche. France has a wide variability in terms of climate influences and topography. Oceanic and degraded oceanic influences meet in Northern France, the south is mainly under a Mediterranean climate and mountain climatic influences are present in the Alps, Pyrenees, and Massif Central (Joly et al. 2010).

A reason that would explain why the quadratic effect of temperature was not revealed in previous studies (Fortin et al. 2009; Feldpausch et al. 2011; Lines et al. 2012; Hulshof et al. 2015; Auger 2016) could be due to the fact that the geographical scope of the data did not cover a sufficient gradient of temperature or that the optimal temperature was not located within this geographical scope. This could be especially true for the study of Fortin et al. (2009) and Auger (2016). Most species in these studies have native ranges that extend further south so that the optimal temperatures may lie somewhere beyond the southern border of Quebec. This might also be the case for some of the seven species that showed a linear temperature effect in this study.

In our data, mean temperature and precipitation from March to September were correlated at -0.52 . Although

this was a moderate level of correlation, it could be argued that the effect is not one of temperature but rather one of precipitation. In all our models, we alternatively tested the temperature and the precipitation when it came to including the climate variables. The idea was to identify which climate variable resulted in the greatest improvement of the model fit before testing the other variable. In the vast majority of cases, including temperature resulted in a greater improvement than including precipitation, with *Quercus ilex* and *Sorbus torminalis* being the two exceptions (Table 3). This result pleads for a greater effect of temperature on tree height when compared to the effect of precipitation. In Spain, the magnitude of the precipitation effect was also found to be smaller than that of the temperature for most species (Lines et al. 2012). On the contrary, Hulshof et al. (2015) found that the height of conifers was more impacted by precipitation than temperature in the USA. However, their models did not account for tree social status or competition from other trees and it can be argued that the significant climate effect they found was partly due to different competition levels and social status along the climate gradient. In our study, we disentangled these effects by including a competition index and a social status index before testing the climate variables.

4.2 Competition effect

The competition has an obvious effect on tree allometry, as shown in Fig. 2. The greater this competition level is, the more slender the trees will be. This effect is a direct consequence of the carbon allocation strategy, which favors height growth before diameter growth (Oliver and Larson 1996, p. 75). Many authors identified this competition effect and took it into account in their models, either through plot basal area or the basal area of larger trees (BAL) (e.g., Temesgen and von Gadow 2004; Garber et al. 2009; Feldpausch et al. 2011; Crecente Campo et al. 2014; Forrester et al. 2017).

In our study, we considered the basal area of other trees since it could hardly be assumed that a particular tree would be competing with itself. More precisely, we wanted to make sure that trees growing alone in their plot would have a competition index of 0, something that is impossible when using plot basal area. During some preliminary trials, we compared the basal area of other trees with plot basal area in terms of model fit. Excluding the target tree from the basal area did not make a big difference in the model fits. However, we decided to keep this competition index since it made more sense from a biological point of view.

The other option would have been to use the BAL competition index. Temesgen and von Gadow (2004) presented the BAL as a convenient index that simultaneously accounts for social status and competition. We rejected this option

because neighbor trees, even if they are smaller in diameter than the target tree, affect crown development through side shading (Oliver and Larson 1996, p. 71). Since the volume increment usually increases from the top of the tree to the base of the live crown (Smith et al. 1997, p. 49), these competitors necessarily affect stem taper and, consequently, the HD relationship. Moreover, there was no reason to assume that social status and competition had a joint effect, so we decided to model them independently.

During preliminary trials, we also tested stem density alone or in interaction with basal area. In either case, this variable did not improve the model fit and, consequently, it was not retained in the model. Some relative density indices also exist (Jack and Long 1996) and could have been used to characterize the competition effect. However, there are two constraints related to the use of those indices: they are usually designed for pure stands and they are not available for all the species we had in this study.

4.3 Social status effect

The social status index was calculated as the ratio between the DBH of the target tree and the mean quadratic diameter (MQD) of its plot. The inclusion of plot MQD in HD relationship models was already found to substantially improve their fit (Saud et al. 2016). In all the models that included this effect, our results showed that the dominant trees tended to be more tapered than trees with a diameter close to the MQD while dominated trees were more slender, a pattern that is typically observed in even-aged stands (Pretzsch 2009, p. 189). For a few species, however, the effect of the social status on tree height was relatively small. This was the case of *Castanea sativa* and *Quercus pyrenaica* (Fig. 3).

Fortin et al. (2009) also found an effect of the social status in their general model of HD relationships in Quebec, Canada. However, their social status index was calculated as the difference between tree DBH and plot MQD and not the ratio between these two variables. Moreover, they did not manage to find an interaction between the social status and the species. In her revision of the model, Auger (2016) found that the social status index based on the DBH:MQD ratio outperformed the difference-based index and had a negative effect on tree height for many species.

During preliminary trials, we compared the two indices and we found out that the ratio was better for some species but worse for others. Globally, the ratio was slightly better than the difference and for this reason, we finally chose to use it. However, there are some issues related to this ratio. First, it is asymmetrical in the sense that dominant trees can exhibit values that are much greater than 1 while dominated trees are by definition bounded between 0 and 1. From a statistical point of view, those dominant

trees growing over a large number of small trees can turn out to be influential observations because of their high leverage. In practice, dominated trees are those that can lose their epinastic control and may expand horizontally instead (Larson 1992). This decrease in apical dominance combined with the development of lateral branches leads to a plagiotropic architecture (Kunstler et al. 2005) that could be overlooked with the ratio-based social index.

Secondly, the ratio-based index assumes that the effect of the social status has nothing to do with tree size. In other words, a tree of 20 cm in DBH growing in a plot with a MQD of 10 cm has the same social status index than a 80-cm tree growing in a plot with a MQD of 40 cm. This assumption is subject to debate and the objective of our study was not to provide a clear answer as to which social index is the best. A thorough comparison between these two social status indices would clearly bring new insights into the morphology of the difference species.

4.4 Slope effect

In their studies, Fortin et al. (2009) and Auger (2016) found a significant effect of the drainage class over tree height, where trees growing in xeric conditions were generally shorter. In this study, we did not have access to the drainage class. However, we found a negative effect of the slope inclination for 31 out of 44 species. The slope and the drainage are dependent. Although the location along the slope plays an important role, the greater the inclination is, the faster the drainage will generally be. Moreover, trees growing on steep slopes have been found to be less sensitive to wind damage (Klaus et al. 2011; Hanewinkel et al. 2014), which could be explained by an acclimation to greater wind stress. Meng et al. (2008) highlighted the negative effect of mean wind speed in the height-diameter relationship of lodgepole pine (*Pinus contorta* Engelm.). In response to the mechanical stress induced by wind bursts, trees usually allocate more resources to diameter growth in order to prevent stem breakage (Bonnesoeur et al. 2016). Unfortunately, we did not have access to wind speeds in our data and, consequently, it was impossible to distinguish this effect from that of the drainage. Information about the topographic location of the plot, such as upper slope, lower slope or flat land, could also be variables of interest for expressing both the wind and the drainage effects. This remains to be investigated.

It could also be argued that the slope inclination is correlated with the temperature since steeper slopes are observed in mountain areas where the temperature is lower. We further investigated the relationship between slope inclination and temperature and obtained a Pearson correlation coefficient of -0.307 , which can be considered as a weak negative correlation.

4.5 Modeling approach

Even though our models included a large array of explanatory variables, a large prediction error remained. As a matter of fact, the root mean square error was larger than 2.0 m for most species (see SM4 in the Supplementary Material). The mixed-model approach we used made it possible to assess the relative contribution of the plot random effect to the total variance of the prediction error. It turned out that this contribution was greater than that of the residual error for trees larger than 20 cm in most cases (see SM5 in the Supplementary Material). The mixed-model approach has been widely used in the context of HD relationships (e.g., Castedo Dorado et al. 2006; Feldpausch et al. 2011; Lu and Zhang 2013; Adamec and Drápela 2016; Kearsley et al. 2017), and the importance of the plot random effects that we found in this study is in accordance with the results of previous studies. For example, Hulshof et al. (2015) showed that R^2 conditional on the random effects predictors were much higher than marginal R^2 . Feldpausch et al. (2011) also outlined the strong influence of the plot random effect on HD allometry.

Plot random effects can be interpreted as one or many unobserved plot-level variables that have a significant effect on the response (Gregoire 1987). Even though our models included plot-level variables such as slope inclination and harvest occurrence, it appeared that they were still far from explaining all of the between-plot variability. During preliminary trials, we tested additional plot-level variables such as soil type and texture but none of them was found to have a significant effect on tree height. Kroon et al. (2008) found a significant effect of the genetic origin on the HD relationships, which could partly explain the between-plot variability we observed. The history of disturbances, whether they be natural or anthropogenic, probably impacts tree allometry as well. However, the availability of the data to account for this history is a major issue.

In this study, we only had access to recent disturbances. When it occurs in the last five years, harvesting can have a significant effect on tree height. However, this effect must be interpreted as a correction for the basal area effect. In spite of our efforts, we did not manage to quantify the impact of natural disturbances on tree height in our models. Fortin et al. (2009) showed that the effect of recent natural disturbances is significant, but smaller than that of recent harvesting in terms of magnitude. Our data covered the 2005–2015 period and only a few large-scale disturbances occurred within this interval. This could explain why our attempts were unsuccessful. We expect that future inventory campaigns will provide additional observations and make the quantification of the effect of natural disturbances possible.

The plot random effect specification in our models is subject to debate. Theoretically, each parameter could

be associated with a plot random effect as suggested by Hall and Bailey (2001). In our study, this means that an additional plot random effect could have been associated with parameter B_{ij} in Eq. 2. However, in practice, this often leads to convergence problems when maximizing the model likelihood (Hall and Bailey 2001). This is precisely what happened for many species in this study and, consequently, we kept the simpler random effect specification shown in Eq. 2. Another option would have been to set the random effect on the model intercept. However, such a random effect specification assumes that the average difference in tree height between two plots is the same regardless of the tree diameters. Actually, it can reasonably be assumed that smaller trees are more alike across the plots than larger trees, which is precisely the reason why we set the plot random effect on parameter A_{ij} . To make sure that this assumption hold, we refitted all the models, but this time with the plot random effect on the intercept. This resulted in a worst fit for all 44 models.

Compared to previous studies on the topic, our study is based on a different model. Many studies relied on the general model $y = A \cdot \text{DBH}^B + \epsilon$. This model is nonlinear and convergence is usually harder to achieve when the model includes random effects. An appealing alternative that was used by some authors consists of linearizing the model as follows: $\ln(y) = \ln(A) + B \cdot \ln(\text{DBH}) + \epsilon$ (e.g., Feldpausch et al. 2011; Chave et al. 2015; Hulshof et al. 2015). The model can then be fitted using a regular linear mixed-effects model. Although this linearized form has some advantages in terms of fitting, it implies a back transformation in order to obtain height predictions on the original scale. A naïve back transformation of log-transformed responses implies a bias and some correction factors are required to obtain unbiased predictions (Duan 1983; Végiard and Ung 1993). Since our model is purely linear, it does not suffer from this back-transformation bias. Moreover, the link between the response variable and the explanatory variables is easier to interpret: the parameters actually represent the change in the response variable caused by a one-unit increase in the explanatory variables.

Our model also makes it possible to test quadratic effects such as those shown in Fig. 5. With the original nonlinear model $y = A \cdot \text{DBH}^B + \epsilon$, this is still possible: parameter A can be replaced by a linear function involving the temperature and the square of the temperature. However, with the log-transformed version $\ln(y) = \ln(A) + B \cdot \ln(\text{DBH}) + \epsilon$, the effects are assumed to be multiplicative (Draper and Smith 1998, p. 278). Quadratic effects such as those shown in Fig. 5 could only be achieved by specifying the temperature and the logarithm of the temperature in the model, which makes the model formulation more complex.

This being said, this linear model of ours is not perfect, and during preliminary trials, we observed that inconsistent

predictions could be obtained when the models of some species were used to generate predictions for trees with diameters below the minimum diameter, i.e., $DBH < 7.5$ cm. Some predictions were actually smaller than 1.3 m. This model misspecification could be corrected by linearly interpolating between the intercept of 1.3 m and the predicted height when $DBH = 7.5$ cm. This remains to be tested and implemented. In the meantime, we recommend not using the models with trees smaller than 7.5 cm in DBH.

We chose to use the temperature and precipitation from March to September because it provided a better fit during preliminary trials. The climate influence could be further refined through a thorough comparison of the available climate variables such as monthly temperatures and precipitations, as well as degree-days. Variables representing the water availability for trees such as soil water balance (Piedallu et al. 2013) could perform better than precipitation. During the preliminary trials, this was not the case, but this might be due to the fact that the spatial distribution of soil water balance remains imprecise.

We did not test stand metrics such as stand age, dominant height, or dominant diameter in our models for several reasons. Age measurements were taken on a very small subsample. Consequently, there was a great deal of uncertainty in the stand age estimates. Dominant heights were also tricky to calculate with the data we had because some heights were unobserved in the 2009 inventory campaign and after. Moreover, testing dominant height in a model of HD relationships when it is calculated with the same height observations that are used to fit the model is a concern from a statistical point of view. In such a context, tree height is both the response variable and an explanatory variable in the model, which leads to overestimate the precision of the predictions (Perron et al. 2009, p. 614). Dominant diameter could have been tested in the model. However, many plots had a mixed composition and some species were only represented by one or a few trees in each plot. The meaning of dominant diameter is questionable in such a context.

5 Conclusions

On the basis of the results of this study, we reached the following conclusions:

- The mean temperature from March to September affected the height-diameter relationship of most species. Although the competition as represented by the basal area of other trees and social status contributed more to the model fit, temperature was not a marginal effect that can be overlooked. It ranked first or second in terms of contribution to the model fit for almost a quarter of the species (Table 4) and the mean predicted

height could change by several meters depending on its values (Fig. 5).

- From a statistical perspective, the temperature effect had a stronger signal than that of precipitation for most species. It was also quadratic, which made it possible to estimate an optimal temperature, i.e., the temperature that maximized tree height, all other things being equal. In most cases of quadratic effects, the average observed temperature from March to September was close to the optimal temperature.
- Under the climate scenario RCP 2.6 and the strong assumptions of stable species distribution, constant form factors and constant forest conditions in terms of competition and social status, two thirds of the species with a climate-sensitive HD relationship would have a reduced height and volume by the end of the twenty-first century.

While the decreases in volume remain relatively small at the local scale, it could have greater impacts at the regional level. Unless these changes are compensated for by the form factors, forest managers should be aware that the volume supply for some valuable species such as *Quercus robur* and *Pinus pinaster* could drop by 3 to 5%, while that of *Fagus sylvatica*, *Picea abies*, and *Abies alba* could increase by 4% by the end of the twenty-first century.

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Data Availability The data used in this study can be made available by the *Institut national de l'information géographique et forestière* (IGN) upon request. The HD relationship models shown in this study were implemented in a Java library which is open-source and freely available at <https://sourceforge.net/p/lerfobforesttools/wiki/FrenchHDRelationships2018/>.

Compliance with Ethical Standards

Conflict of Interest None.

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